The neural signatures of social hierarchy-related learning and interaction: a coordinate- and connectivity-based meta-analysis

Author names and affiliations

Siying Li[1†], Frank Krueger[2,3†], Julia A. Camilleri[4,5], Simon B. Eickhoff[4,5], Chen Qu[1*]

[1] Key Laboratory of Brain, Cognition and Education Sciences, Ministry of Education, School of Psychology, Center for Studies of Psychological Application, and Guangdong Key Laboratory of Mental Health and Cognitive Science, South China Normal University, China;

[2] School of Systems Biology, George Mason University, Fairfax, VA, USA;

[3] Department of Psychology, George Mason University, Fairfax, VA, USA;

[4] Institute for Neuroscience and Medicine (INM-7), Research Center Jülich, Germany;

[5] Institute for Systems Neuroscience, Medical Faculty, Heinrich-Heine University Düsseldorf, Germany;

[†] The authors contributed equally to this work

[*] Corresponding author: Chen Qu, Dr. School of Psychology, South China Normal University, Guangzhou, 510631 China.

E-mail address: fondest@163.com

20

Abstract

Numerous neuroimaging studies have investigated the neural mechanisms of two mutually independent yet closely related cognitive processes aiding humans to navigate complex societies: social hierarchy-related learning (SH-RL) and social hierarchy-related interaction (SH-RI). To integrate these heterogeneous results into a more fine-grained and reliable characterization of the neural basis of social hierarchy, we combined coordinate-based meta-analyses with connectivity and functional decoding analyses to understand the underlying neuropsychological mechanism of SH-RL and SH-RI. We identified the anterior insula and temporoparietal junction (dominance detection), medial prefrontal cortex (information updating and computation), and intraparietal sulcus region, amygdala, and hippocampus (social hierarchy representation) as consistent activated brain regions for SH-RL, but the striatum, amygdala, and hippocampus associated with reward processing for SH-RI. Our results provide an overview of the neural architecture of the neuropsychological processes underlying how we understand, and interact within, social hierarchy.

Keywords: social hierarchy; meta-analysis; meta-analytic connectivity modeling; resting-state functional connectivity; functional decoding

Introduction

Social hierarchies — referring to a coherent and accepted rank of a group of individuals along one or more social dimensions — are ubiquitous in the biological world (Qu et al., 2017). This rank always has a close link with ones' grasp of resources (Berger, et al., 1980). Thus, social hierarchy implied valuable information for individual well-being, socializing, and development (Boyce, 2006; Cheng et al., 2013; Sapolsky, 2005). Given its complexity as well as its importance and pervasiveness to human society, the human need to understand social hierarchies around them and use the knowledge to guide their social life. This also gains an advantage for social hierarchical structure and makes it fluent social stimuli that are processed more easily in cognitive processing of seeing, understanding, learning, and remembering, compared with other types of social structures, such as more flat structures (Zitek & Tiedens, 2012). Meanwhile, as a common social organization, social hierarchy provides a strong force to natural selection. Individuals who display a superior ability in understanding social hierarchy and modifying behavior consequently can often be found to gain an edge in terms of survival and development (Gilbert, 2000; Boyce, 2004; Sapolsky, 2005; Cheng et al., 2013; Watanabe & Yamamoto, 2015). Two mutually independent yet closely related cognitive processes play crucial roles in aiding humans to navigate complex societies: (i) the process of social hierarchy learning and (ii) the process of social hierarchy guiding behaviors and social interaction (Chiao et al., 2008; Watanabe and Yamamoto, 2015; Olsson et al., 2020). Numerous studies have used neuroscientific techniques to investigate the neural mechanisms involved in these two forms of social hierarchy-related processes. The goal of the current meta-analysis study was to reveal their neural mechanisms by answering the following two questions: How is social hierarchical knowledge acquired by individuals? How is the social hierarchy used to modulate behaviors and interactions?

59   The following section will elaborate on these two fundamental social hierarchy-related processes —

60   *social hierarchy-related learning* (*SH-RL*) and *social hierarchy-related interaction* (*SH-RI*).

61   **1. SH-RL phase**

62   The ability to obtain social hierarchical knowledge enables social species to overcome the pressures

63   of navigating a fast-changing and complex society (Insel & Fernald, 2004). One of its primary

64   contributions is in aiding decisions that engage fundamental modes of social interaction such as fight

65   or flight decisions in animals and whether to compete or cooperate in humans. Social hierarchy

66   learning paves the way for subsequent behaviors and social interactions.

67   Both animals and humans can obtain social hierarchical knowledge to guide their behaviors

68   through dominance cues, dyadic competition, and observational learning (Fernald, 2014; Qu et al.,

69   2017). Detecting social rank by interpreting dominance cues could be regarded as a rapid locating

70   process, which is more automatic, such as forming an initial impression of others' social rank through

71   physical characteristics or appearance. Multiple sources of information such as body size, facial

72   features, emotional expressions, postures, and occupational status contribute to social hierarchy

73   detecting at a glance (Chiao et al., 2008, 2009; Mattan et al., 2017). For instance, owners of luxury

74   sports cars must be rich men, and realizing this fact is not costly. Developmental studies have shown

75   that even infants can derive dominance information from some dominance cues (Cummins, 2000;

76   Boyce, 2004; Brey & Shutts, 2015; Charafeddine et al., 2015). Moreover, an event-related potentials

77   (ERP) brain study has indicated that people can perceive dominance cues from aggression-related

78   emotional expressions in the early temporal stages of information processing and detect social

79   dominance cues from facial expressions later on (Chiao et al., 2008). Another study probed the neural

80   electrophysiological responses of participants to faces accompanied by information of occupational

81   social status and found that faces with high-status occupation elicited a larger late positive potential

82   (LPP) (Breton et al., 2019). Through rapid evaluation, individuals appear to be able to detect the

83   social position of others and rapidly adjust subsequent behaviors.

84   Since dominant cues are insufficient in understanding complicated hierarchical relationships

85   within intricate human social networks (Todorov et al., 2008; Kumaran et al., 2012), humans also

86   employ a more refined updating process which dynamically constructs social hierarchical structure in

87   their mind through learning the feedback of the binary comparison in a goal-directed manner. Direct

88   (e.g., competition) and indirect (e.g., observational learning) comparisons are two ways in which a

89   precise and explicit social hierarchical map can be formed. Direct competition leads to the emergence

90   of social hierarchy (Fernald, 2014; Qu et al., 2017), with potentially high risk and high loss, which is

91   the only way to inverse or change the inherent hierarchical structure (Paz-y-Miño et al., 2004; Fernald,

92   2014;). The indirect comparison refers to inferring target information through observation. Many

93   species including nonhuman primates, rats, and birds have abilities to make transitive inferences, and

94   it has also been reported that fish learn hierarchical relationships by observing conflicts around them

95   (McGonigle & Chalmers, 1977; Roberts & Phelps, 1994; Bond et al., 2003; Grosenick et al., 2007).

96   The brain circuits involved in the process of rapidly locating social hierarchy information and

97   the more refined process of updating social hierarchy information have been well documented in

98   previous research (Qu et al., 2017). The *first process* is rapid and involves the detection of social

99   hierarchy cues and mapping dominance cues to social hierarchical structures. Detection is a major

100   neural function supported by the salience network which may also serve to detect dominance cues for

101   this rapid locating process (Bressler & Menon, 2010; Menon, 2015). One study using a facial

102   judgment task found that, relative to simple perceptual judgments of facial features, judgments of

103   social dominance activated hub regions associated with the salience network and the anterior insula

104   (AI) in particular (Smith et al., 2016).

105   The *second process* includes dynamic updating which is driven by feedback-based trial-by-trial

106   learning. Those hidden features of updating and computing let researchers link this process to neural

107   computational modeling. Researchers have applied both reinforcement learning (RL) and Bayesian

108   computational models to uncover the neural mechanism for the updating process of social dominance

109   learning (Kumaran et al., 2016; Ligneul et al., 2016). RL models emphasize the process of creating

110   relationships between stimuli and outcomes, which can be applied for social hierarchy learning

111   (Suzuki, 2012; Seo & Lee, 2017; Qu et al., 2017). In contrast, Bayesian approaches emphasize

112   decision making via probabilistic representations of the world (Knill & Pouget, 2004; Khalvati et al.,

113   2016; Annis & Palmeri, 2017; Baker et al., 2017), and social hierarchy can be considered as a hidden

114   variable that can be learned through the likelihood of observation (Qu et al., 2017; FeldmanHall &

115   Shenhav, 2019). As a powerful tool to reveal the process of encoding, the neurocomputational

116   approach provided more essential knowledge on this issue. In terms of observational learning, the

117   medial prefrontal cortex (mPFC) is engaged in the learning of rank, computing estimates of the rank

118   of others, and updating knowledge about one's own place in the hierarchy (Kumaran et al., 2016).

119   With regards to dyadic competition, the rostromedial PFC (rmPFC) is thought to represent social rank,

120   while the ventromedial PFC (vmPFC) and striatum encode successes and failures, respectively

121   (Ligneul et al., 2016) — emphasizing the foundational role of the mPFC in dynamic updating.

122   To establish the social hierarchical structure in one's own social knowledge frame, the

123   hippocampus and intraparietal sulcus region (IPS) are credited respectively for cognitive processes

124　abut structure and magnitude — functions closely linked with mental constructing and representing of

125　social hierarchy (Cohen et al., 2007; Tavares et al., 2015).

126　　　Overall, based on previous research, the learning phase of social hierarchy presumably depends

127　on three functions and its corresponding supporting brain regions: (i) detecting (AI); updating

128　(mPFC), and representing (hippocampus and IPS) of social hierarchy information.

129　**2. SH-RI phase**

130　In daily life, social hierarchical information serves to guide adaptive behaviors and thus promotes a

131　more harmonious social existence. Behaviors and interactions in society modulated by social

132　hierarchy have been observed in humans (i.e., adults but also children) as well as nonhuman primates.

133　These behaviors and interactions have been found to touch on a wide range of cognitive functions,

134　including attention, socio-emotional functioning, and decision-making (Dugatkin & Alan, 1997;

135　Gianaros et al., 2008; Boksem et al., 2012; Breton et al., 2014; Santamaria-Garcia et al., 2014; Feng

136　et al., 2015, 2016; Hu et al., 2014, 2016).

137　　　For example, a study on empathy found that empathic responses to the pain of others are

138　modulated by social hierarchy — showing activities in AI and medial cingulate cortex as a function of

139　social status (Feng et al., 2016). Further, in the ultimatum game, people with high social status are

140　more likely to reject unfair offers — mirrored by activities in the amygdala and thalamus — than

141　those from a lower status (Hu et al., 2016). Moreover, after learning the hierarchical structure of

142　employees from two companies, people were asked to judge which company these persons belong to.

143　Although this simple task did not explicitly require any knowledge about rank, however, activities in

144　the amygdala and anterior hippocampus generated rank-related signals automatically (Kumaran et al.,

145   2016).

146   Some researchers suggested that the dominance of higher status may be associated with the

147   processing of reward (Zink et al., 2008; Freeman et al., 2009; Ly et al., 2011; Santamaría-García et al.,

148   2015). For example, an association between neural responses to social hierarchy and brain

149   morphology was reported in the caudate nucleus — a region implicated in reward processing —

150   combining ERP with structural MRI (Santamaría-García et al., 2015). Superior rank faces compared

151   with inferior rank faces induced a larger N170 component, implying a higher sensitivity in the

152   striatum to superior social rank. The same pattern of asymmetric value assignment according to social

153   rank can be observed in nonhuman primates. For example, monkeys sacrifice juice rewards to view

154   the faces of high-status monkeys despite being thirsty but require juice payment to view the faces of

155   low-status monkeys (Deaner et al., 2005).

156   Overall, based on previous evidence, the impacts of social hierarchy on interactions and

157   behaviors are probably mediated by (i) reward processes (e.g., striatum) and additional processes

158   regulating the reward circuit (e.g., amygdala, hippocampus).

159   **3. The present study**

160   A plethora of studies in the field of social hierarchy learning and interacting provide the opportunity

161   for deeper exploration. One issue that might arise from various tasks or paradigms that have been

162   employed to investigate social hierarchy is the possibility that unrelated activation mingled in the

163   target neural mechanism in a single study. While in the meantime, the neural patterns produced by

164   these key processes that occur consistently across studies must be characterized in some quantitative

165   way. Another issue that remains open is the underlying psychological functions of brain regions or

networks engaged in social hierarchy-related processing. Thus, we implemented a meta-analysis approach that was designed to quantitatively synthesize previous neuroimaging findings regarding the two social hierarchy-related processes: SH-RL and SH-RI. By integrating neuroimaging studies that have investigated these processes, we can gain a more reliable and precise picture of the neural basis of how humans understand and respond to social hierarchy.

In this study, we implemented separate neuroimaging meta-analyses to explore the two neural mechanisms supporting SH-RL and SH-RI. First, we identified the consistent activated brain region associated with two social hierarchy-related processes by conducting coordinate-based meta-analyses using an activation likelihood estimation (ALE) approach (Eickhoff et al., 2009). Second, we investigated the connectivity among brain regions by performing task-based meta-analytic connectivity mapping (MACM) and task-free resting-state functional connectivity (RSFC). Finally, based on a large-scale database, we employed functional decoding (FD) on mental processes associated with identified regions to understand their psychological functions (Bellucci et al., 2020).

Methods

1. Meta-analysis

1.1. Literature search and selection

First, we performed a literature search of online databases including PubMed, ISI Web of Science, and Google Scholar. The following relevant topic items were entered into these databases: social hierarchy, social rank, social status, social standing, social-economic status, and dominance. These were combined with the following terms describing measurement technique terms: fMRI, functional MRI, and PET. In addition, we also searched bibliographies and citation indices in pre-selected papers.

187   Studies generated from these searches were further assessed according to the following criteria

188   (**Fig. 1**): (i) research content correlated with social hierarchy; (ii) fMRI or PET was used as the

189   imaging modality; (iii) subjects were free from psychiatric and neurological diagnoses; (iv) whole-

190   brain general-linear-model-based analyses (rather than a region of interest [ROI] analyses) were

191   applied; (v) activation was presented in a standardized stereotaxic space (Talairach or Montreal

192   Neurological Institute, MNI). Using GingerALE software with Brett's mni2tal algorithm, a

193   conversion to the MNI coordinates was employed for studies that reported in Talairach coordinates

194   (Lancaster et al., 2007).

195
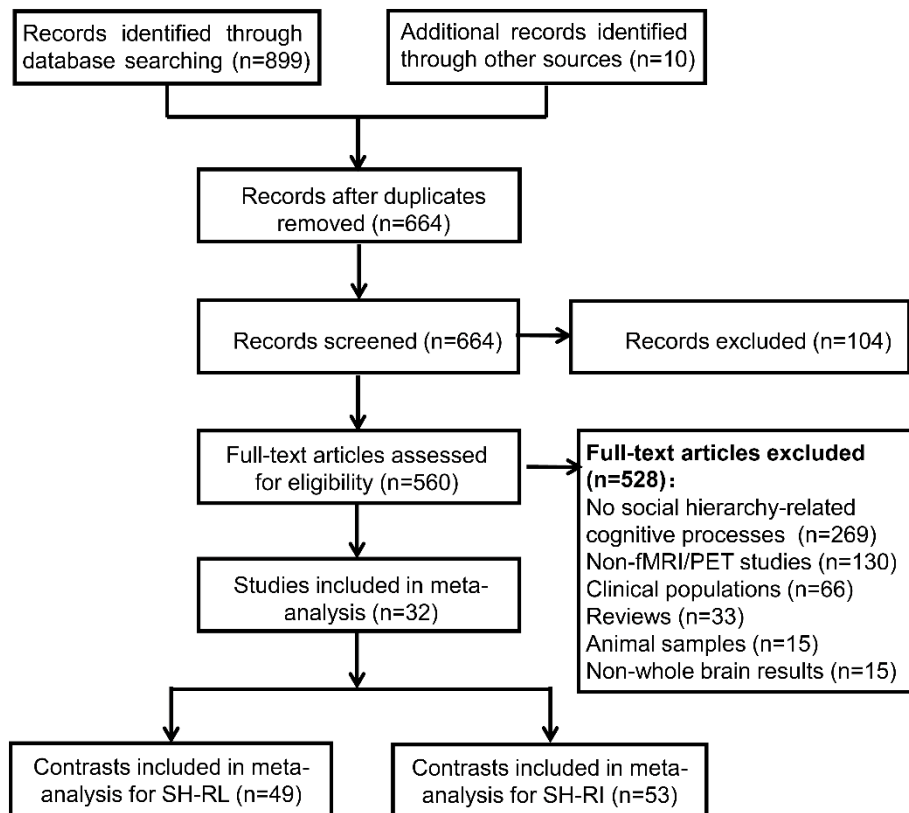
196   **Figure 1. Flowchart of literature search and selection for meta-analysis.**

197   *SH-RL, social hierarchy-related learning; SH-RI, social hierarchy-related interaction.*

198

Articles that fulfilled the above criteria were assigned — either to SH-RL or SH-RI — based on

the category of cognitive processing induced by experimental tasks. Since some studies included

more than one task and explored both modes of processing, experiments of these studies were

assigned separately according to the mode of processing (SH-RL vs. SH-RI). We labeled in this study

any process of judging or estimating the position of others within a social hierarchy through various

forms of information as the process related to SH-RL. SH-RL describes the transition of social

hierarchy knowledge from unknown to known or from vagueness to clarity. During this phase,

participants often need to produce a judgment, estimation, or choice regarding the social rank of

others in the experimental context. As the second process of interest, SH-RI examined or described

any process that involved interacting within a social hierarchy environment. SH-RI implies that an

individual's activities or behaviors are, in some way, modified by the social hierarchy. For instance,

social hierarchy information is the known condition within the experimental setting or has been

learned by participants, and the influence of social hierarchy is the primary focus in this process.

By applying a filter on search results according to the inclusion/exclusion and category criteria,

we were left with a total of 32 published studies. Thirteen of these studies examined the process of

SH-RL and 22 examined the process of SH-RI (**Table 1**).

215   **Table 1.** Summary of studies included for the coordinate-based meta-analysis

Study	N	Task	Contrast
Social hierarchy-related learning			
Ligneul et al. (2016)	28	competitive task	parametric analysis, correlation with positive competitive prediction errors
			parametric analysis, correlation with negative competitive prediction errors
			parametric analysis, correlation with social dominance status
			intermediate opponent win (control failure) > intermediate lose (control success)
Kumaran et al. (2016)	28	transitive inference task	parametric analysis, correlation with the difference in power (test trials)
			parametric analysis, correlation with hierarchy update index (training trials)
			parametric analysis, correlation with hierarchy update index in the self condition (training trials)
			parametric analysis, negative correlation with entropy over item pairs (training trials): main effect self and other
			parametric analysis, positive correlation with entropy over item pairs (training trials): main effect self and other
			parametric analysis, chosen power (training trials): main effect of self and other conditions

			parametric analysis, chosen power in the self condition (training trials)
			parametric analysis, chosen power in the other condition (training trials)
			parametric analysis, chosen power (training trials): self > other condition
Kumaran et al. (2012)	25	transitive inference task	parametric analysis, correlation with the inference score index in the social condition
			parametric analysis, correlation with the inference score index in the social > non-social condition
			parametric analysis, correlation with correct probability in the social condition
			parametric analysis, correlation with correct probability in the social > non-social condition
Kishida et al. (2012)	27	Ranked group IQ task	rank_beginning > rank_end
			parametric analysis, negative correlation with the rank change
			parametric analysis, positive correlation with the rank change
Cloutier et al. (2013)	13	self-referential social status judgment task	status type by status level interaction
			status type main effect
			status level main effect
Farrow et al. (2011)	22	facial viewing task	social hierarchy > fame, age, gender and 'number. higher / lower'
Chiao et al. (2008)	7	facial viewing task	dominant > neutral faces

			submissive > neutral faces
Marsh et al. (2009)	30	status poses viewing task	hierarchy cue
			hierarchy cue $\times$ stimulus gender
			hierarchy cue $\times$ stimulus gender $\times$ subject gender
			hierarchy cue $\times$ subject gender
Smith et al. (2016)	23	social judgment task	social judgment > perceptual judgment
Freeman et al. (2009)	34	display viewing task	dominant > subordinate
			social hierarchy (dominant, subordination) $\times$ culture (Japanese, American)
Chiao et al. (2009)	12	comparison task	uniform comparison
			face comparison
			car comparison
			uniform distance
			face distance
			car distance
			number (close-far) > face (close-far)

			uniform (close-far) > number (close-far)
			face (close-far) > number (close-far)
			face (close-far) > car (close-far)
			car (close-far) > number (close-far)
			car (close-far) > uniform (close-far)
			car (close-far) > face (close-far)
Mason et al. (2014)	19	status judgment task	status judgments > weight judgments
Haaker et al. (2016)	23	observation of confrontations	parametric analysis, correlation with dominance rank
			parametric analysis, correlation with increasing hierarchy knowledge

Social hierarchy-related interaction

Feng et al. (2016)	22	sensory stimulation viewing	superior > inferior
			inferior > superior
			(inferior_pain − inferior_no pain) > (superior_pain − superior_no pain)
			(inferior_Pain − Inferior_no pain) < (superior_pain − superior_no pain)
Op de Macks et al. (2017)	58	jackpot task	social rank feedback > monetary gain feedback

			social rank feedback > monetary loss feedback
			social rank play > monetary play
Kim et al. (2016)	28	infant cry paradigm	socioeconomic status effect
Kim et al. (2015)	40	infant cry paradigm	socioeconomic status×gender in (baby cry − white noise)
Zheng et al. (2017)	72	allocate money task	low rank (unfair − fair) − high rank (unfair − fair)
			unfair low rank (reject − accept) − unfair high rank (reject − accept)
			unfair high rank (reject − accept) − unfair Low rank (reject − accept)
Muscatell et al. (2018)	23	face observation task	correlation with subjective social status in black faces observe > white faces observe
			correlation with subjective social status in black faces observe > baseline
			correlation with subjective social status in white faces observe > baseline
Kumaran et al. (2016)	28	categorization task	correlation with person rank
Zink et al. (2008)	24	reaction time task	superior player > inferior player
Zink et al. (2008)	24	visual discrimination task	superior player > inferior player
			subject lost and inferior won > subject lost and inferior lost
			subject won and superior lost > subject won and superior won

Ligneul et al. (2017)	28	passive presentation task	superior faces > inferior faces
Kumaran et al. (2012)	25	bid task	parametric analysis, correlation with person rank
Hu et al. (2016)	23	ultimatum game	(low status unfair > low status fair) > (high status unfair > high status fair)
			high status unfair > low status unfair
Erk et al. (2002)	12	attractiveness rating task	sports cars> small cars
			sports cars> limousines
			limousines > sports cars
			limousines> small cars
Cloutier et al. (2014)	20	impression formation task	status type×status level
			status type main effect
			status level main effect
Sheridan et al. (2012)	18	stimulus response learning task	high socioeconomic status (novel rule> familiar rule) > low socioeconomic status (novel rule> familiar rule) (all trial)
			low socioeconomic status (novel rule> familiar rule) > high socioeconomic status (novel rule> familiar rule) (all trial)
			high socioeconomic status (novel rule> familiar rule) > low socioeconomic status (novel rule>

			familiar rule) (early trial)
			low socioeconomic status (novel rule> familiar rule) > high socioeconomic status (novel rule> familiar rule) (early trial)
Mattan et al. (2018)	60	face viewing task	perceived status main effect (negative correlation with external motivation, with internal motivation covariate)
			perceived status main effect (negative correlation with external motivation, without internal motivation covariate)
			perceived status main effect (negative correlation with internal motivation, with external motivation covariate)
			perceived status main effect (negative correlation with internal motivation, with external motivation covariate)
			race $\times$ status
Kim et al. (2013)	49	emotion regulatory task	positive correlation with the family income-to-needs ratio in the reappraise‐maintain
Noble et al. (2006)	38	letter string one-back task	socioeconomic status $\times$ phonological awareness
Muscatell et al. (2016)	31	social stress task	negative correlation with subjective social status
			positive correlation with subjective social status
Cloutier et al. (2012)	19	impression formation task	high>low morale status

			low>high financial status
			low>high financial status
Quirin et al. (2013)	17	movie watching task	power motive viewing
Haaker et al. (2016)	23	confrontation task	fear acquisition with dominant face > no fear acquisition with intermediate face (categorial)
			fear acquisition with subordinate face > no fear acquisition with intermediate face (categorial)
			fear acquisition dominant face > no fear acquisition with intermediate face (change over time)
			fear extinction dominant face > fear extinction subordinate face
			fear acquisition with dominant face > fear acquisition with subordinate face (reinstatement)

216   N,   number   of   participants

217

1.2. Activation likelihood estimation (ALE) analysis

219   We conducted a coordinate-based meta-analysis by using the ALE algorithm (GingerALE software,

220   version 3.0.2) (Eickhoff et al., 2009). This algorithm identified areas that showed convergence of foci

221   across different functional or structural experiments to obtain brain regions with a spatial association

222   that was higher than random (Turkeltaub et al., 2002; Laird et al., 2005). This method treats reported

223   foci not as single points, but rather as spatial three-dimensional Gaussian probability distributions.

224   Widths of foci were based on empirical estimates of the spatial uncertainty based on the between-

225   subject and between-template variability of the neuroimaging data (Eickhoff et al., 2009).

226   Individual modulated activation (MA) map was created firstly by taking the maximum

227   probability associated with any one focus (the closest one) for each voxel within each included

228   experiment (Turkeltaub et al., 2012). This modified ALE algorithm was able to reduce the influence

229   of multiple foci from a single on individual MA value of a single voxel (Turkeltaub et al., 2012). Next,

230   a union of individual MA maps was generated across selected studies by computing it against a null-

231   distribution of random spatial associations between studies using a non-linear histogram integration

232   algorithm (Eickhoff et al., 2012; Turkeltaub et al., 2012). The resulting p value maps were thresholded

233   using the cluster-level family-wise error (cFWE) correction at $p < 0.05$ with a cluster defining

234   threshold of $p < 0.001$ and 10,000 permutations (Eickhoff et al., 2012).

235   A total of 49 experiments (i.e. contrasts) examined the process of SH-RL (261 foci, 1,044

236   subjects, average of 21.3 subjects per experiment) and a total of 53 experiments examined the process

237   of SH-RI (282 foci, 1,656 subjects, average of 31.2 per experiment).

238 *1.3. Conjunction and contrast analyses*

239 To explore convergences and differences between the meta-analytic findings of SH-RL and SH-RI,

240 we conducted conjunction and contrast analyses. The conjunction analysis was performed by applying

241 the minimum conjunction of ALE results of SH-RL and SH-RI with a cFWE < 0.05 and a voxelwise,

242 cluster-forming threshold of $p < 0.001$ (Nichols et al., 2005).

243   Next, contrast analyses were conducted to identify the statistically significant differences in the

244 convergence between SH-RL and SH-RI. Contrast analyses were based on voxelwise differences of

245 ALE maps of SH-RL and SH-RI. To test its statistical significance, permutation tests were conducted

246 as follows. All foci contributing to these two ALE maps were pooled and randomly divided into two

247 groups of the same size as the original data sets (Eickhoff et al., 2011). Based on each new data set, an

248 ALE image was created, then subtracted from the other and compared with the original data. After

249 25,000 times permutations, a null-distribution of difference in the ALE values between two SH-RL

250 and SH-RI was created. Then the true difference in the ALE values was examined against the voxel-

251 wise null-distribution, yielding a p value for the difference at each voxel under label exchangeability.

252 The resulting p values were thresholded at a posterior probability of $p > 95\%$ for true differences and

253 with an additional cluster extent threshold of cluster size > 200 mm^3.

254 **2. Functional connectivity analyses**

255 *2.1. Task-based connectivity: meta-analytic connectivity modeling (MACM) analyses*

256 MACM analyses were performed to examine functional co-activation patterns of pre-defined ROIs

257 involved in SH-RL and SH-RI (Note that we extracted brain regions of the meta-analytic clusters as

258 ROIs.) (Robinson et al., 2010; Eickhoff et al., 2011; Langner et al., 2014). To do this analysis, whole-

brain peak coordinates from all eligible studies, i.e. whole-brain neuroimaging studies reporting

activation in standard stereotaxic space in a healthy population, were downloaded from BrainMap

(http://www.brainmap.org/) if at least one focus of activation within each ROI was reported. Studies

that investigated effects on age, sex, handedness, and interventions (e.g., pharmacological or training-

based), as well as clinical populations, were excluded. Coordinates were then analyzed using the ALE

algorithm to detect areas of convergence of co-activation with each seed. Finally, the ALE maps were

thresholded using a cFWE correction ($p < 0.05$) with a cluster-forming threshold of $p < 0.001$ using

10,000 permutations for correcting multiple comparisons.

Information of MACM analyses — i.e., ROI, the number of experiments, subjects, and foci that

the functional co-activation pattern produced for each ROI — were included as follows: ROIs related

to SH-RL consisted of left amygdala/hippocampus cluster (L amygdala/hippocampus) (338

experiments, 5,112 subjects, 4,099 foci), right amygdala/hippocampus cluster (R

amygdala/hippocampus) (316 experiments, 4,900 subjects, 3,712 foci), medial prefrontal cortex

(mPFC) (143 experiments, 2,173 subjects, 1,766 foci), left anterior insula (LAI) (581 experiments,

8,661 subjects, 8,803 foci), right anterior insula (RAI) (406 experiments, 6,140 subjects, 5,924 foci),

left intraparietal sulcus region (LIPS) (407 experiments, 5,940 subjects, 5,878 foci), right intraparietal

sulcus region (RIPS) (250 experiments, 3,789 subjects, 3,643 foci) and right temporo-parietal junction

(RTPJ) (96 experiments, 1,389 subjects, 1,412 foci). ROIs related to the SH-RI consisted of L

amygdale/hippocampus (212 experiments, 3,340 subjects, 2550 foci), R amygdale/hippocampus (280

experiments, 4,394 subjects, 3391 foci), left fusiform gyrus (LFG) (194 experiments, 2,676 subjects,

2,884 foci) and striatum (214 experiments, 3,635 subjects, 2,994 foci).

2.2. Task-free connectivity: resting-state functional connectivity (RSFC) analyses

281 RSFC analyses were run separately using the same ROIs as for the MACM analyses as seed regions.

282 These analyses were based on resting-state fMRI images of 192 healthy volunteers obtained from the

283 enhanced Nathan Kline Institute-Rockland Sample (NKI-RS: http://fcon_1000.projects.nitrc.org

284 /indi/enhanced/) (Nooner et al., 2012). The sample of enhanced NKI-RS is representative of the

285 general population across age, ethnicity, and socioeconomic status (Horn & Blankenburg, 2016). The

286 enhanced NKI-RS dataset has been widely used by many meta-analysis studies and made numerous

287 contributions to RSFC analyses (Krall et al., 2015; Gu et al., 2019; Wong et al., 2019). Functional

288 images were acquired by a Siemens TimTrio 3 T scanner using a gradient-echo, echo-planar imaging

289 (EPI) pulse sequence with repetition time = 1.4 s, echo time =30 ms, flip angle = 65, voxel size = 2.0

290 $\times$ 2.0 $\times$ 2.0 mm; number of slices = 64.

291   Using FIX (FMRIB's ICA-based Xnoiseifer, version 1.061 as implemented in FSL 5.0.9)

292 (Griffanti et al., 2014; Salimi-Khorshidi et al., 2014), physiological and movement artifacts were

293 removed from the resting-state data by decomposing the data into independent components and

294 identifies noise components employing a large number of distinct spatial and temporal features via

295 pattern classification. Unique variance related to the artefactual independent components was

296 regressed from the data together with 24 movement parameters (including derivatives and second-

297 order effects as previously described and evaluated; cf. Satterthwaite et al., 2013). Using SPM8

298 (Wellcome Trust Centre for Neuroimaging, London) and in-house Matlab scripts, images were then

299 further preprocessed as following described. The first four scans were excluded before further

300 analyses, the remaining images were corrected for head movement using a two-pass (alignment to the

301 initial volume followed by alignment to the mean after the first pass) affine registration. For each

302 subject, the mean image was spatially normalized to the ICBM-152 reference space using the "unified

303   segmentation" approach (Ashburner & Friston, 2005).

304   Applying resulting deformation parameters, the individual functional images were subsequently

305   smoothed with a 5-mm full width at half maximum Gaussian kernel to improve the signal-to-noise

306   ratio and compensate for residual anatomic variations. The time-course of each seed was extracted by

307   computing the first eigenvariate of the time-series of all voxels within 5 mm of the seed coordinates.

308   Variance explained by the mean white matter and cerebral spinal fluid signal were removed from the

309   time series to reduce spurious correlations, which was subsequently band-pass filtered preserving

310   frequencies between 0.01 and 0.08 Hz. The functional connectivity map of each seed was correlated

311   with the time-series of all other gray-matter voxels across the brain using Pearson correlation.

312   Correlation coefficients were transformed into Fisher's z-scores, which were entered in a second-level

313   ANOVA for group analysis, including age and sex as covariates of no interest. Statistical significance

314   was assessed by non-parametric permutation-based inference and cluster-level thresholded at $p < 0.05$

315   to correct for multiple comparisons.

316   ***2.3. Consensus connectivity maps***

317   The following analyses were performed to explore the functional connectivity networks by

318   identifying the brain regions that are strongly connected to multiple brain regions as defined by ALE

319   analyses. It is defined as brain areas that showed robust connectivity with multiple consensus

320   functional connectivity maps generated by conjunction analyses of MACM and RSFC for each ROI.

321   Specifically, based on MACM and RSFC analyses, task-dependent and task-independent whole-brain

322   functional connectivity maps were generated for each ROI for SH-RL and SH-RI separately. For each

323   ROI, the conjunction map between MACM and RSF was generated by using the minimum statistic

324   approach (Nichols et al.,2005) — leading to eight connectivity maps for SH-RL and four for SH-RI,

325   showing the brain areas consistently interacting with each ROI across rest and task states (cf. Clos et

326   al., 2014; Hardwick et al., 2015). Finally, functional connectivity networks involved in processes of

327   SH-RL and SH-RI delineated by identifying all regions that were significantly connected with

328   multiple ROIs, specifically the brain regions in which overlapped with the consensus connectivity

329   maps of at least half of the ROIs with an additional extent-threshold of 10 continuous voxels

330   (Camilleri et al., 2018; Amft et al., 2014).

331   **3. Functional decoding (FD) analysis**

332   Functional decoding was run for the same ROIs that were identified in ALE analyses. The function

333   profile of each ROI of SH-RL and SH-RI were characterized based on behavioral domain meta-data

334   categories in the BrainMap database (http://brainmap.org/scribe/). These categories describe the

335   experimental properties of each study stored in the database according to different mental processes,

336   such as action, emotion, cognition, perception, and interoception (Turner & Laird, 2012). The

337   individual functional profile corresponding to each ROI was determined by using the forward

338   inference approach —providing information about the probability of identifying activity in a brain

339   region given previous knowledge of a psychological process. Specifically, forward inference tested

340   whether the conditional probability of activation given a particular behavioral domain i.e.

341   P(Activation|Behavioral domain) was higher than the baseline probability i.e. P(Activation).

342   Significance was determined by a binomial test with a standard $\alpha=0.05$, corrected for multiple

343   comparisons using the false discovery rate (FDR) method.

344   **4. Anatomical labeling and data visualization**

345   The SPM Anatomy toolbox (www.fz-juelich.de/ime/ spm_anatomy_toolbox, v.2.2b, Eickhoff et al.,

346   2007) and MRIcron (http://people.cas.sc.edu/rorden/mricron/install.html/) were used for anatomical

347   labeling. MRIcroGL (https://www.mccauslandcenter.sc.edu/mricrogl/home/) was used for brain

348   visualizations.

349

Result

351   Results for the meta-analyses are reported separately for the social hierarchy-related learning and

352   interaction phase.

353   **1. Results for SH-RL phase**

354   *1.1. Results for ALE analysis*

355   The ALE analysis for SH-RL revealed significant convergence of activation in the following regions:

356   mPFC, L amygdala/hippocampus, R amygdala/hippocampus, LIPS, RIPS, LAI, RAI, and RTPJ (**Fig.**

357   **2a, Table 2**).

358
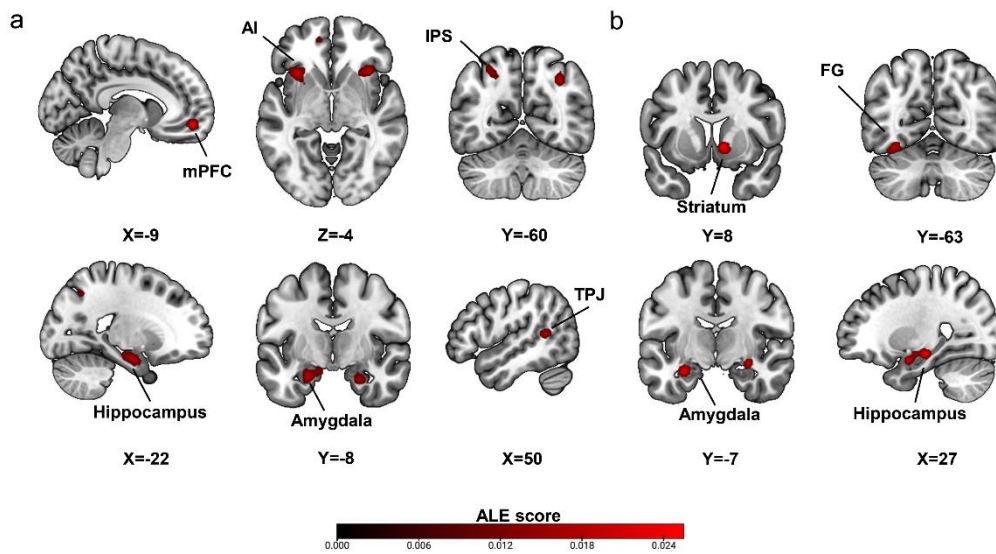
Figure 2. Social hierarchy-related brain regions.

ALE meta-analysis results showing brain regions consistently engaged for (A) social hierarchy-related learning and (B) social hierarchy-related interaction. Results were cluster-level familywise-error corrected for multiple comparisons (cFWE < 0.05 with a cluster defining threshold of p < 0.001 and 10,000 permutations). L, left; R, right; mPFC, medial prefrontal cortex; AI, anterior insula; IPS, intraparietal sulcus; TPJ, temporo-parietal junction; LFG, left fusiform gyrus.

Table 2. ALE meta-analysis results for social hierarchy-related learning and interaction

Brain Region Labels	Anatomical location	BA	MNI Coordinates x	y	z	Z score[*]	Cluster Size (mm³)
Social hierarchy-related learning							
L Amygdala/ Hippocampus	Amygdala/ Hippocampus	34/28	-24	-12	-20	4.90	2152
R Amygdala/ Hippocampus	Amygdala/ Hippocampus	34/28	24	-10	-26	4.46	1944

mPFC	Medial frontal gyrus	32/10	-10	52	-10	5.85	1400
LAI	Insula	13	-34	20	-2	5.76	1392
RAI	Insula	13	34	22	-6	4.86	888
LIPS	Superior parietal lobule	7	-30	-58	52	4.07	1024
RIPS	Superior parietal lobule	7	32	-62	42	4.76	872
RTPJ	Superior temporal gyrus	39	48	-50	10	4.40	832
Social hierarchy-related interaction							
L Amygdala/ Hippocampus	Amygdala/ Hippocampus	28/34	-28	-8	-20	4.97	1632
R Amygdala/ Hippocampus	Amygdala/ Hippocampus	/	-26	-20	-14	4.97	1032
LFG	Fusiform gyrus	37/19	-32	-66	-14	4.08	952
Striatum	Caudate/Putamen	/	10	8	-4	5.11	792
Contrast: SH-RL>SH-RI							
LIPS	Superior parietal lobule	7	-20	-63	45	2.64	960
LAI	Insula	13	-28	22	0	2.71	840
RAI	Insula	/	28	24	-6	2.10	352
mPFC	Medial frontal gyrus	32/10	-10	48	-14	2.42	592
L Hippocampus	Hippocampus	28/34/35	-20	-18	-20	2.41	424
L Amygdala	Amygdala	34/28	-14	-2	-22	2.35	336
R Amygdala	Amygdala	34	18	4	-16	2.10	232
RTPJ	Superior temporal gyrus	22	52	-46	10	2.00	288
Contrast: SH-RI>SH-RL							
R Amygdala/ Hippocampus	Amygdala/ Hippocampus	28	30	-14	-12	2.39	840
Striatum	Caudate/Putamen	/	6	6	-2	2.18	704
LFG	Fusiform gyrus	19	-28	-64	-18	2.45	312
Conjunction						ALE ($\times 10^{-2}$)	
L Amygdala/ Hippocampus	Amygdala/ Hippocampus	/	-24	-8	-20	1.86	288
R Amygdala/ Hippocampus	Amygdala/ Hippocampus	34/28	22	-4	-20	1.65	176

368   *ALE, activation likelihood estimation; MNI, Montreal Neurological Institute; L, left; R, right;*

369   *mPFC, medial prefrontal cortex; LAI, left anterior insula; RAI, right anterior insula; L*

370   *Amygdala/ Hippocampus, left Amygdala/ Hippocampus cluster; R Amygdala/ Hippocampus, left*

1.2. Results for consensus connectivity maps

Results from MACM and RSFC analyses and their conjunctions for each ROI are displayed in **Fig. S1**. For mPFC, the connectivity results were consistent with the activation patterns of the default network. With regards to bilateral AI — the core region of the salience network — we found a clear similarity between its functional connectivity pattern and that of the salience network. L amygdala/hippocampus and R amygdala/hippocampus revealed similar functional connectivity patterns with mPFC, posterior cingulate, bilateral inferior frontal gyrus, striatum, bilateral fusiform gyrus. LIPS and RIPS both showed a pattern of connectivity with bilateral middle frontal gyrus, bilateral dorsal anterior cingulate cortex, bilateral middle occipital gyrus, bilateral middle temporal gyrus, bilateral inferior temporal gyrus. For RTPJ, it showed a pattern of connectivity with bilateral middle frontal gyrus, bilateral middle temporal gyrus, and middle cingulate cortex.

Next, regions supporting SH-RL were identified that were robustly connected with multiple seed regions: bilateral AI, bilateral anterior cingulate cortex (ACC), bilateral dorsolateral prefrontal cortex (DLPFC), posterior parietal cortex (PCC), bilateral middle frontal gyrus, and bilateral fusiform gyrus (FG) (**Fig. 3**).
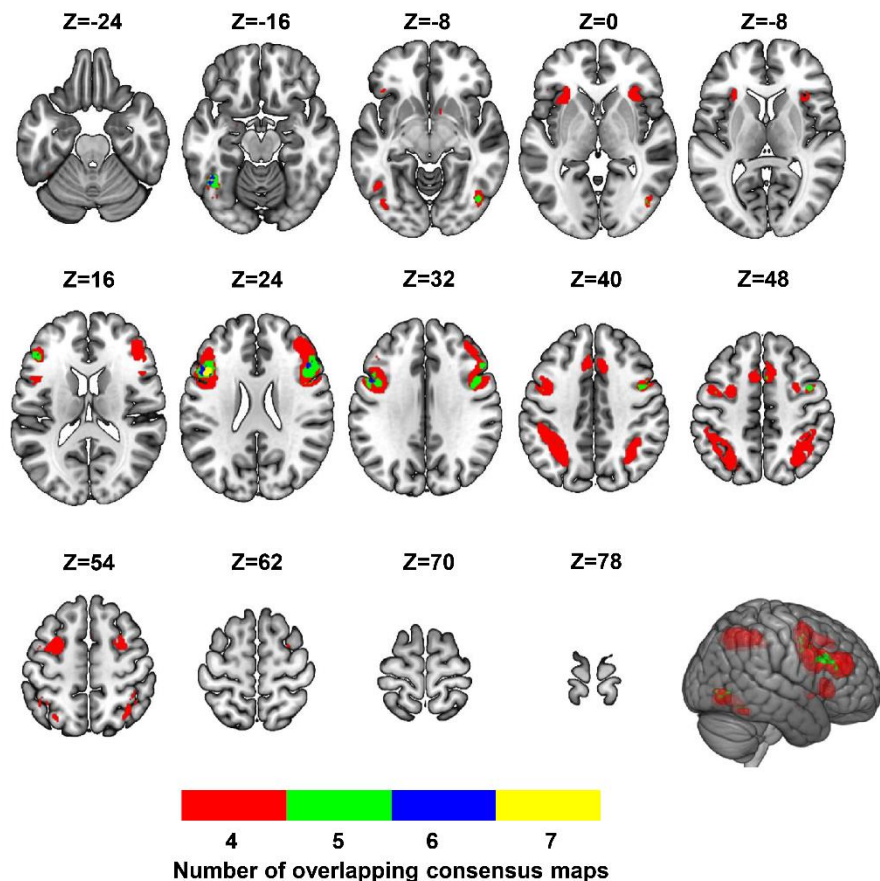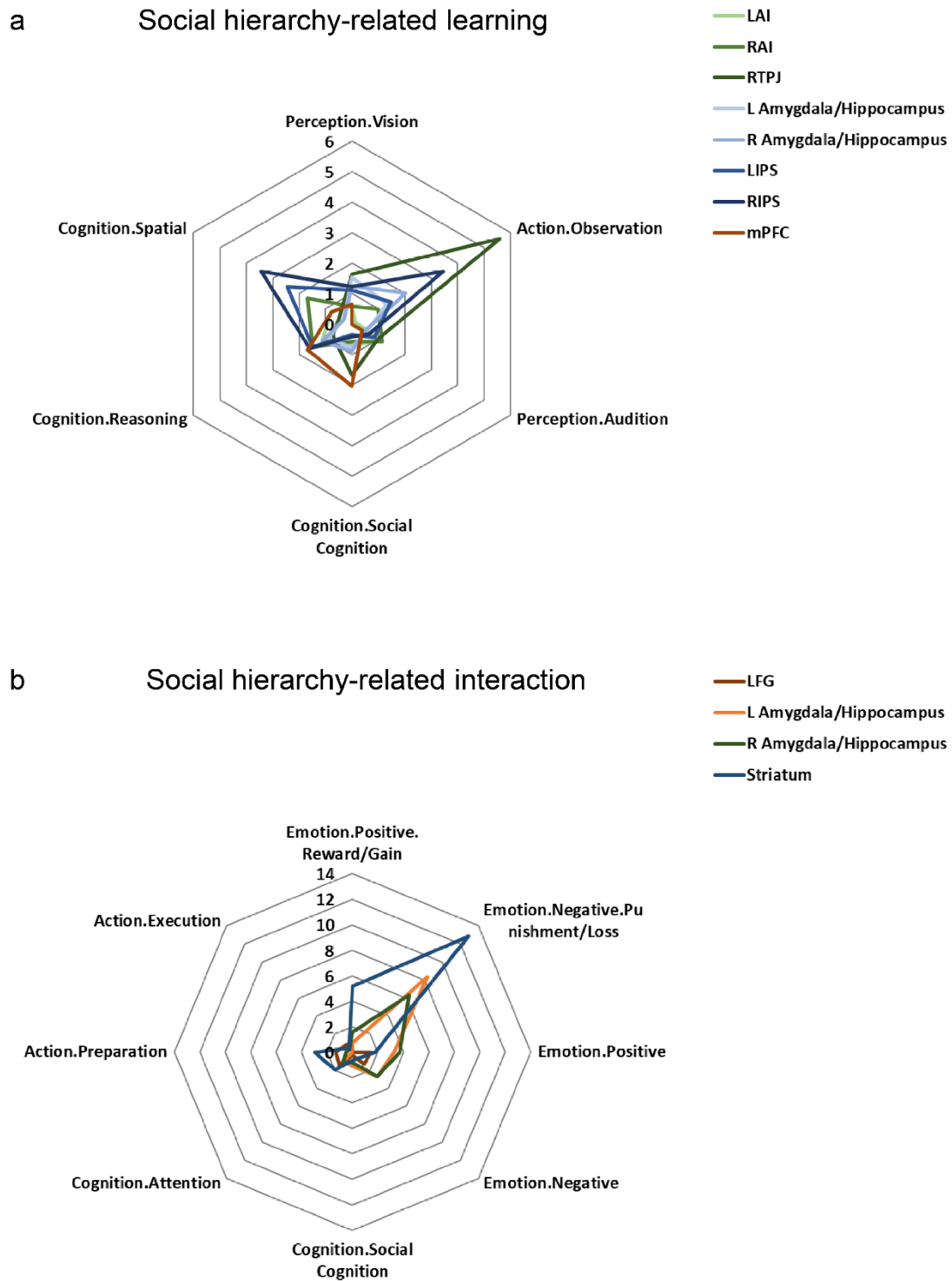
Figure 3. Consensus connectivity maps of social hierarchy-related learning.

Consensus connectivity maps identified by overlapping task-free (RSFC) and task-based (MACM) connectivity maps in the process of social hierarchy-related learning.

1.3. Results for FD analysis

Functional decoding analyses were performed to gain insights about the psychological functions of the identified regions (**Fig. 4a**). With the hypothesis of the main cognitive function involved in SH-RL, how closely related the three main functions (detection, updating and computation, and construction and representation) and brain regions were brought into focus. Results revealed that LAI, RAI, and RTPJ had a close link with observation in the action domain as well as vision and audition

402   in the perception domain, the behavioral domains that related to detection. The mPFC was

403   functionally associated with processes of high-order cognition including social cognition and

404   reasoning in the cognition domain, which was in accord with the assumption that mPFC supports

405   social hierarchical information updating and computation in SH-RL. L amygdala/hippocampus, LIPS,

406   RIPS had close associations with the visuospatial cognition, i.e., spatial in the cognition domain,

407   which had a close link to the mental operation of integrating scattered social hierarchy knowledge to

408   the social hierarchy structure in one's mind. All results that survived after correction (FDR< 0.05) are

409   reported in **Fig. S2**.

a　　Social hierarchy-related learning

Legend:
- LAI
- RAI
- RTPJ
- L Amygdala/Hippocampus
- R Amygdala/Hippocampus
- LIPS
- RIPS
- mPFC

Axes: Perception.Vision, Action.Observation, Perception.Audition, Cognition.Social Cognition, Cognition.Reasoning, Cognition.Spatial

b　　Social hierarchy-related interaction

Legend:
- LFG
- L Amygdala/Hippocampus
- R Amygdala/Hippocampus
- Striatum

Axes: Emotion.Positive.Reward/Gain, Emotion.Negative.Punishment/Loss, Emotion.Positive, Emotion.Negative, Cognition.Social Cognition, Cognition.Attention, Action.Preparation, Action.Execution

410

Figure 4. Functional decoding (FD) analyses to characterize the functional roles of meta-analytic clusters consistently involved in the processing of social hierarchy-related learning (SH-RL) and social hierarchy-related interaction (SH-RI).

414   *(A) For SH-RL, the value of likelihood ratios in FD depicted the weight of each brain region on three*

415   *main functions involved in SH-RL: detection (perception.vision; action.observation;*

416   *perception.audition), updating, and computation (cognition. social cognition; cognition. reasoning),*

417   *construction and representation (cognition. spatial). (B) For SH-RI, the value of likelihood ratios in*

418   *FD depicted the weight of each brain region on some basic behavioral domains involved in SH-RI, i.e.*

419   *action (execution; preparation), cognition (attention; social cognition), and emotion (positive;*

420   *negative; positive. reward/gain; negative. punishment/ loss). L Amygdala/ Hippocampus, left*

421   *amygdala/hippocampus cluster; R Amygdala/Hippocampus, right amygdala/hippocampus cluster;*

422   *mPFC, medial prefrontal cortex; LAI, left anterior insula; RAI, right anterior insula; LIPS, left*

423   *intraparietal sulcus region; RIPS right intraparietal sulcus region; RTPJ, right temporo-parietal*

424   *junction; LFG, left fusiform gyrus.*

425

426   **2. Results for social hierarchy-related interaction phase**

427   *2.1. Results for ALE analysis*

428   For the ALE analysis, significant convergence of activation was observed in L

429   amygdala/hippocampus, R amygdala/hippocampus, LGF, and striatum (**Fig. 2b, Table 2**).

430   *2.2. Results for consensus connectivity maps*

431   Results of MACM and RSFC and their conjunctions for each ROI can be found in Figure 4. Striatum

432   produced functional connectivity patterns with the thalamus, midbrain, bilateral inferior frontal gyrus,

433   bilateral medial frontal gyrus, and middle cingulate cortex. For LFG, it is found that the patterns of

434   connectivity with bilateral inferior occipital gyrus and bilateral superior parietal lobule. Bilateral

435   amygdala/hippocampus clusters revealed functional connectivity with mPFC, posterior cingulate,

436   bilateral inferior frontal gyrus, striatum, and bilateral fusiform gyrus.

437   Next, the brain network supported SH-RI was identified by searching brain regions that were robustly

438   connected with multiple seed regions. It is found that many brain regions of overlapped consensus

439   connectivity map located in the reward circuit, including the striatum, medial orbitofrontal cortex

440   (mOPC) which implied the close link between SH-RI and reward circuit. Results of overlapping two

441   and three consensus connectivity maps were illustrated in **Fig. 5**. No brain regions survived after the

442   number of consensus connectivity maps overlapped increase to four.

443
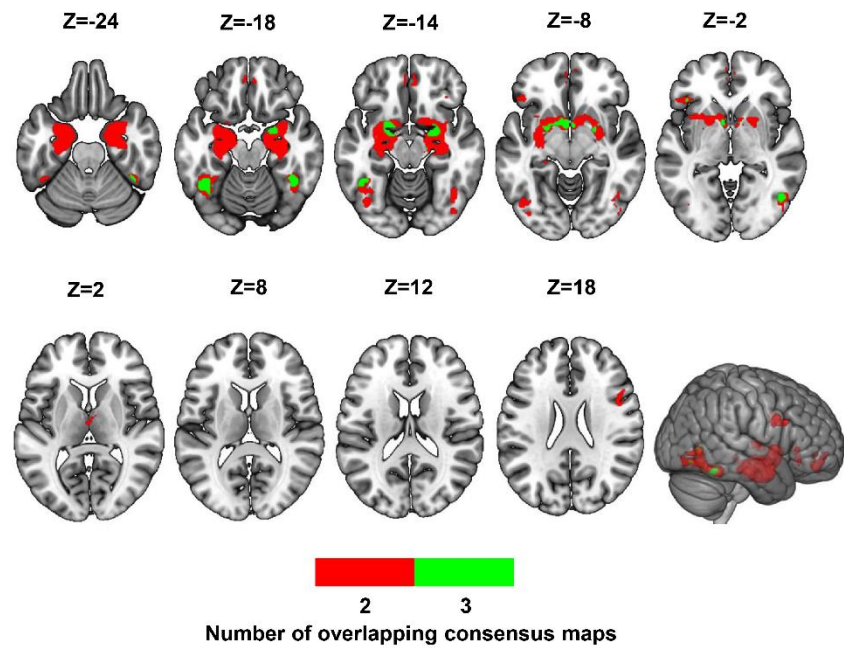
444   **Figure 5. Consensus connectivity maps of social hierarchy-related interaction.**

445   *Consensus connectivity maps identified by overlapping task-free (RSFC) and task-based (MACM)*

446   *connectivity in the process of social hierarchy-related interaction.*

447

2.3. Results for FD analysis

449   To explore the underlying psychological function of meta-analytic brain regions engaged in SH-RI,

450   the likelihood ratios of some main behavioral domains in each ROI were determined (**Fig. 4b**). In a

451   broad sense, many psychological functions, such as action, cognition, and emotion can be influenced

452   by social hierarchy. To characterize the functional profile of the meta-analytic clusters in SH-RI, some

453   basic domains received attention including execution and preparation in the action domain, attention

454   and social cognition in the cognition domain, and positive, negative, reward/gain, and

455   punishment/loss in the emotion domain. High likelihood ratios of some psychological domains in

456   multiple ROIs illustrate the importance and consistency of their roles in SH-RI. Results showed that

457   among these basic psychological domains, striatum and bilateral amygdala/hippocampus clusters

458   were closely related to the domains of reward/gain as well as punishment/loss which implied the close

459   links between reward-related psychological functions with SH-RI. All results that survived after

460   correction (FDR<0.05) are reported in **Fig.S1**.

461

462   **3. Results for contrast and conjunction analyses**

463   For the contrast analyses, LIPS, bilateral AI, mPFC, left amygdale/hippocampus clusters and RTPJ

464   were more consistently activated in SH-RL compared to SH-RI, whereas striatum, LFG, and right

465   hippocampus were more consistently activated in SH-RI compared to SH-RL (**Fig. 6a, Tab.1**). The

466   conjunction analysis showed a common activation maximum in the bilateral amygdala/hippocampus

467   clusters (**Fig. 6b, Table 2**).
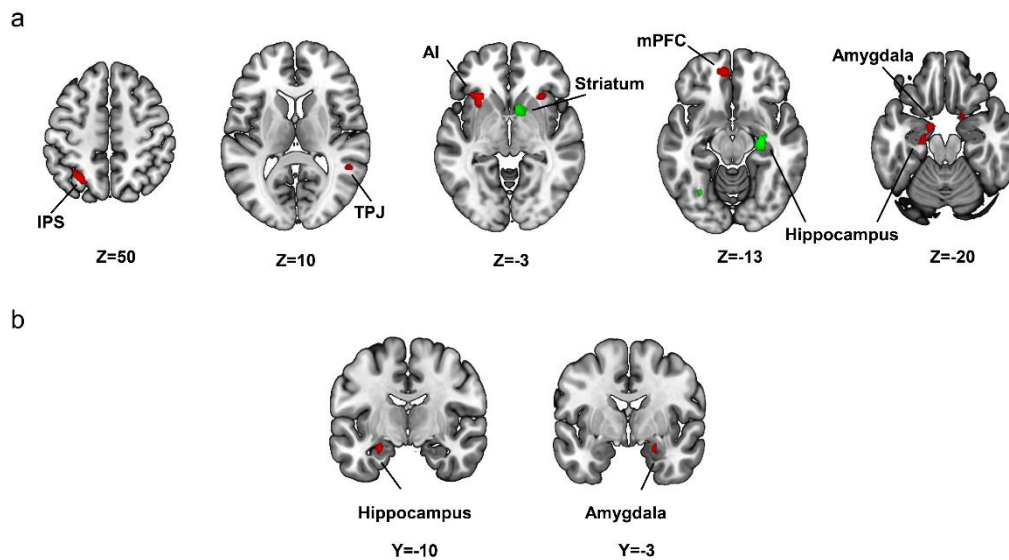
Figure 6. Significant clusters from conjunction and contrast analyses.

Results of contrast analysis (A) and conjunction analysis (B). Brain regions showing higher consistent activation in the social hierarchy-related learning are illustrated in red, whereas regions showing higher consistent activation in the social hierarchy-related interaction are illustrated in green. L, left; R, right; mPFC, medial prefrontal cortex; AI, anterior insula; IPS, intraparietal sulcus; TPJ, temporo-parietal junction; LFG, left fusiform gyrus.

Discussion

The role of social hierarchy cannot be overstated in its importance. In addition to acting as a guide to social interactions and improving the survival prospects of individuals within it, social hierarchy also contributes greatly to stability and harmony within societies. Given the significance of social hierarchy, there is much to be gained by endeavoring to understand more about how humans create and work within them. The pace of this quest has increased since the advancement of functional

482   neuroimaging techniques and has allowed us to develop insights into the neural underpinnings of how

483   humans understand and interact with social hierarchies. However, the wide variety of experimental

484   tasks that have been employed by these studies means that results are somewhat heterogeneous. As a

485   consequence, in the absence of any systematic framework of analysis, it is not possible to identify the

486   core neural mechanisms which remain significant even if specific experimental situations change.

487   To synthesize previous findings, we divided paradigms into two distinct domains: those that

488   examine the process of SH-RL (i.e. social hierarchy-related learning) and those that examine the

489   process of SH-RI (i.e. social hierarchy-related interaction). Further, we used quantitative meta-

490   analyses to reveal the neural mechanisms that support these two processes. Using the ALE method,

491   we identified brain regions that were consistently engaged by these cognitive processes and examined

492   their underlying functional connectivity networks as generated by task-based co-activation (i.e.,

493   MACM) and task-free connectivity analyses (i.e., RSFC). Then we conducted functional decoding

494   analyses which provided us with a sound basis for speculation regarding the functional roles of these

495   regions.

496   In general, we made the following observations. For SH-RL we found that AI and TPJ were

497   associated with the detection of dominance cues and that the mPFC plays an important role in

498   updating and computing dynamic social hierarchy information. These regions may be used to

499   construct a social hierarchy structure with the support of IPS, amygdala, and hippocampus. With

500   regards to SH-RI, we found that the modulation of the social hierarchy may have strong associations

501   with the reward network. Supports in regulating behaviors could be traced to the striatum, amygdala,

502   and hippocampus. With the framework of analysis described, we will discuss the results within the

503   context of the two above processes and their relationship based on conjunction and contrast analyses.

1. SH-RL phase

We found that the process of SH-RL elicited consistent activation patterns in the following brain regions: mPFC, RTPJ, and amygdala, hippocampus, IPS, and AI. Based on the results of MACM, RSFC, and FD, we will discuss how these brain regions relate to SH-RL within the context of three main functions: detection, updating and computation, and construction and representation.

1.1. Detection

The ability to detect valid cues carrying social hierarchy information represents an important starting point to the process of obtaining knowledge about social hierarchy. Extrapolating from our findings, we argue that bilateral AI may serve this role for the two following reasons. Based on our task-based co-activation and task-free connectivity analyses, we found that the pattern of its functional connectivity was consistent with that of the salience network. This finding underlined the important link between AI and this network. From a constant stream of incoming sensory inputs, the salience detection mechanism in this network dynamically selects specific stimuli for additional processing (Menon, 2015). As a prominent node of the salience network, a main function of AI in the salience network is the detection of relevant stimuli (Crottaz-Herbette & Menon, 2006; Seeley et al., 2007; Sterzer & Kleinschmidt, 2010). Researchers have found that AI contributes to detection in many tasks examining numerous cognitive domains (Swick et al., 2011; Menon, 2015). Facial features are the most likely candidate to act as valid stimuli for providing information about one's social status. One study used a forced-choice task based on human faces to reveal brain regions engaged in social hierarchy comparison. After controlling for confounding factors, including the age of targets, gender, and fame, activation of AI (Brodmann 47) remained significant for social hierarchy discrimination

525   (Farrow et al., 2011). Based on such evidence combined with our current findings, we confirmed that

526   the detection function of AI acts on a wide spectrum of mental processes including the acquisition of

527   social hierarchy knowledge.

528   In the process of obtaining social hierarchy knowledge, the role of TPJ seems related to the

529   detection of social dominance cues. Functional profiling of TPJ revealed its role involved in

530   observation and perception. This result is consistent with previous research. Meta-analysis studies

531   found that TPJ has an influential role in the detection of extraneous stimuli and reorienting of

532   attention (Decety & Lamm, 2007; Krall et al., 2014). Therefore, we suggest that TPJ serves to detect

533   relevant information about social hierarchy when individuals attempt to clarify hierarchical

534   relationships.

535   *1.2. Updating and computation*

536   Obtaining social hierarchy knowledge through dominance cues represents only one component of

537   what is required to navigate the human social landscape. Sometimes these clues are fuzzy or even

538   contrived (Kumaran et al., 2012). It seems that almost all creatures, whether human or animal, are

539   born knowing how to camouflage themselves behind external characteristics. Thus, a more refined

540   process is necessary to build a more precise model of social hierarchy structures. Competition and

541   observational learning are ways in which more precise information about the positions of others

542   within social hierarchies can be obtained. Successful learning supported by these two modes requires

543   outcome to be tracked and knowledge of one's social rank to be updated. The core factor underlying

544   this ability is that of internal updating and computation. Our functional connectivity and functional

545   decoding analyses gave us a clear indicator of the importance of mPFC in this role. Function profiles

546   revealed its role associated with computation and updating, such as social cognition and reasoning.

547   Thus, we argue that the ability to compute and update information about social hierarchies can be

548   attributed to mPFC.

549   In many studies, mPFC is credited with internal computation. A model-based fMRI study found

550   that mPFC tracked and updated the rank of opponents (Ligneul et al., 2016). Moreover, mPFC is the

551   only brain region that has been found to encode prediction errors, a cognitive component that

552   promotes information updating, implying mPFC contribution to updating variations between

553   predictive outcome and reality (Ligneul et al., 2016). Although a different task and model framework

554   was used, another study supports this function in mPFC. Based on Bayesian approaches, when

555   participants compared the ranks of strangers through observation and inference, mPFC was engaged

556   in computing estimates of their power and updating information about one's own rank within the

557   hierarchy (Kumaran et al., 2016).

558   The internal updating and computation function of mPFC is not restricted to the domain of social

559   hierarchy. It has been found to make similar contributions across numerous studies examing social

560   domains including those examining social norms (Xiang et al., 2013), learning about ownership

561   (Lockwood et al., 2018), tracking of expertise or ability (Boorman et al., 2013; Wittmann et al., 2016),

562   and mentalizing (Hampton et al., 2008). In general, based on neural computations, many studies have

563   found that internal computing signals are correlated with activation in mPFC, highlighting its function

564   in information updating and computation.

565   *1.3. Construction and representation*

566   The ultimate purpose of the process of SH-RL is to accurately construct or represent social

567 hierarchical relationships in one's own mind. Brain regions involved in this function are thought to

568 reflect the degree of social hierarchy by activation level characteristics. That is, social hierarchical

569 stimuli should induce regular activation in these brain regions as opposed to an irregular signal. This

570 regularity should be correlated with the rank within the social hierarchy of an object. Based on our

571 results and previous findings, this process may recruit several brain regions including the

572 hippocampus, IPS, and amygdala.

573   Combined with previous findings and our functional decoding analysis, it is found that the role

574 of IPS and the hippocampus have a close link with visuospatial cognition. In addition to physical

575 space, these two areas are also sensitive to the encoding of social space (Parkinson et al., 2014;

576 Montagrin et al., 2017). Moreover, previous studies have found that their cortical activity is a function

577 of rank within the social hierarchy (Chiao et al, 2009; Kumaran et al., 2012, 2016; Haaker et al.,

578 2016).

579   The hippocampus represents a kind of neural navigation system which helps us to map not just

580 spatial dimensions but also abstract concepts and social relationships (Tavares et al., 2015;

581 Constantinescu et al., 2016; Schafer & Schiller, 2018;). To investigate how the brain responds to

582 ongoing changes in social relationships such as modulations across affiliation and dominance

583 dimensions, one fMRI study recorded neural activity while participants interacted with other roles.

584 They found that perception of social navigation was closely related to the hippocampus (Tavares et al.,

585 2015). This finding of the hippocampus provided a possible explanation for questions about why the

586 hippocampus working prominently in some studies about social hierarchy (Kumaran et al., 2012;

587 Zink et al., 2008). Social hierarchy learning is processing like building social relationship structure in

588 mind constantly where may the role of hippocampus comes into play. This is one possible reason for

589   the phenomenon that the hippocampus parametrically tracked the degree of the rank of target stimuli.

590   IPS also appears to play a significant role in the construction and representation of relationships

591   within the social hierarchy. It has been found that activation levels in IPS correlate with the social

592   status of targets when performing a self-referential status judgment task (Cloutier & Gyurovski, 2013).

593   Moreover, literature exploring how IPS encodes social space has provided clues as to how it may

594   construct models of social structure. One study used multivoxel pattern analysis to reveal the neural

595   mechanism underlying how distance is processed across spatial, temporal, and social domains. This

596   study found that IPS was engaged across all distance domains at an above-chance level (Parkinson et

597   al., 2014). This finding illustrated the functional integration capability of IPS in processing features of

598   dimension across both physical and social space. Social hierarchy is, conceptually, a kind of ordering

599   or ranking based on one social dimension or combined social values. In this way, the IPS may play a

600   role in processing information to determine superiority/inferiority of rank, a process that requires the

601   computation of magnitude judgments or encoding of relationships in social space.

602   Amygdala has also been found to be associated with the representation of the social hierarchy.

603   Activation in the amygdala appears to scale linearly with the rank within a social hierarchy (Kumaran

604   et al., 2016; Haaker et al., 2016). For example, in one study, participants were required to learn the

605   rank of others through observation of confrontation. This study revealed that the gradual acquisition

606   of social hierarchy knowledge was negatively associated with amygdala responsivity. That is,

607   increasing rank discrimination predicted decreasing levels of activation in the amygdala (Haaker et al.,

608   2016). In contrast to the representation of hierarchical relationships by IPS and hippocampus, the

609   amygdala only showed sensitivity to social space and not to physical space (Kumaran et al., 2012,

610   2016). The representation of social hierarchy in amygdala may stem from the sensitivity to different

levels of emotion and motivation which is related to social rank. For example, research on non-human

primates showed that surgical lesions on amygdalae resulted in diminished social status and increased

submissiveness (Rosvold et al., 1954). The role of amygdala in motivation and emotion may not only

support learning about social hierarchy but may also offer to play a role in maintaining status

(Rosvold et al., 1954; Kumaran et al., 2012; Watanabe & Yamamoto, 2015).

2. SH-RI phase

Cognitive processes related to social hierarchy involve obtaining information and subsequently this

information guiding or impacting behaviors and social interactions. On the basis of acquired

knowledge about social hierarchy, behaviors can be modified in ways consciously and unconsciously.

Our findings revealed roles for striatum, amygdala, hippocampus, and LFG in this process of social

hierarchy-related interaction.

2.1. Overlap with the reward circuit

According to our functional connectivity results, we found many brain regions of overlapped

consensus connectivity maps located in the reward circuit. Moreover, for three main regions, bilateral

amygdala/hippocampus cluster and striatum, functional decoding indicated an association of their

function with reward and punishment. These findings suggest that modulation of SH-RI may not be

independent of reward processing. Furthermore, these results could not be explained by the presence

of financial incentives that were offered by experimenters to increase engagement in participants.

Experimental tasks in most previous studies were not directly relevant to monetary reward (Freeman

et al., 2009; Haaker et al., 2016; Feng et al., 2016). Thus, the inducing factor of reward processing

should be hidden in social hierarchical information itself. Exploring the effects of social hierarchy on

632   behavior and social interaction from a reward processing perspective would be helpful in furthering

633   our understanding.

634   Previous studies demonstrated that the striatum is one of the key structures in the reward

635   network and that amygdala, hippocampus are key components in regulating this network (Haber &

636   Knutson, 2009). The significant role of the striatum in rewarding processing cannot be isolated from

637   the synergy of other structures. The convergent fibers from the cortex within the striatum along with

638   hippocampal, amygdalo-striatal, and other projections make striatum a key entry port for processing

639   emotional and motivational signals and thus driving action output in the basal ganglia (Russchen et al.,

640   1985; Fudge & Haber, 2001; Friedman et al., 2002; McFarland & Haber, 2002 Haber & Knutson,

641   2009). A variety of aspects of reward processing can be mediated by this complex neural network

642   formed by connectivity between these brain regions.

643   Striatum, which can represent primary reinforcers is also sensitive to higher-order rewards

644   including social comparisons, social hierarchy, and reputation (Kedia et al., 2014; Christopoulos et al.,

645   2017). For example, when participants viewed players who ranked by stars, their striatum responded

646   to the higher one with a greater degree of activation compared with the lower one (Zink et al., 2008).

647   This can help individuals to interact with others from different ranks in an appropriate way.

648   The functions of brain regions can sometimes be express through their interaction. The role of

649   amygdala in regulating reward processing has been demonstrated in numerous studies, in part through

650   observations of critical interactions between it and striatum in forming stimulus-reward associations

651   (Baxter & Murray, 2002). Hippocampal input to the shell of the nucleus accumbens is important for

652   driving nucleus accumbens activity. Moreover, activity-dependent modulation of the strength of this

653 input may be involved in the regulation of goal-directed behaviors (Legates et al., 2018).

654 Communication among these brain regions mentioned above in both function and structure plays an

655 integral role in reward processing and may explain a variety of phenomena.

656 *2.2. Impacts of social hierarchy guided by social reward*

657 As a basic principle of behavior, rewards are crucial for many activities including incentive learning,

658 comparing social information, forming appropriate responses to stimuli, and developing goal-directed

659 behaviors (Haber & Knutson, 2009; Kedia et al., 2014; Fareri & Delgado, 2014). Although the effect

660 of social hierarchy is numerous and complicated, with the principle of reward guiding, we can

661 summarize the intricate situations as follows: those of superior rank attract more cognitive resources

662 and gain more positive feedbacks compared with those of a relatively inferior rank (Dalmaso et al.,

663 2011; Khalvati et al., 2016). For example, interviewers can obtain information about the social class

664 of candidates and make inferences about the fit, competence, starting salary, and signing bonus in

665 ways that bias the process in favor of applicants of higher social class (Kraus et al., 2019). In a

666 competition task, participants strategically adjusted themselves by improving their performance when

667 facing strong opponents (Ligneul et al., 2016). Many studies have observed parallel effects in the

668 neural system. By using a competitive reaction time task within the context of both stable and

669 unstable social hierarchy structures, many brain regions such as the striatum, occipital gyrus,

670 parahippocampal gyres showed stronger activation when faced with opponents of a high rank (Zink,

671 et al., 2008). It is reasonable to assume that, compared with those of an inferior rank, individuals of

672 superior rank have a greater social influence. Such superiority often implies a higher threat in

673 competition or higher benefit in cooperation, thus mobilizing more cognitive resources to interact

674 with them carefully is adaptable.

675   With evidence from another direction, we become more convinced that rewarding guide the

676   influence of social hierarchy on behaviors and interactions: if the reward behind the social rank

677   change, the effect of social rank change accordingly. Western culture tends to reinforce dominant

678   behaviors, whereas Eastern culture tends to reinforce subordinate behavior (Freeman et al., 2009).

679   This well-established cross-cultural difference in behavior has been verified by self-reports of

680   participants (Freeman et al., 2009). The different reward signal underlying this characteristic behavior

681   of social hierarchy between cultures was expressed on a neural level by the mesolimbic reward

682   system (Freeman et al., 2009). In participants from the USA, dominant stimuli selectively engaged the

683   caudate nucleus and mPFC, whereas these same regions were selectively engaged by subordinate

684   stimuli in participants from Japan (Freeman et al., 2009). In a social status task, the results didn't

685   show a significant status-relative value assignment in the striatum but reflect an interaction between

686   agent's status and subject's own status: subjects with high social status had a higher degree of

687   activation for high-status agents which is opposite to low-status subjects, they have a higher

688   activation to low-status agents in striatum (Ly et al., 2011). In other words, subjects showed an equal

689   rank preference. In nonhuman primates, one study also found a similar pattern of preference for equal

690   rank. Specifically, high-status monkeys preferentially attended to others with high-status, whereas

691   low-status monkeys attend to other low-status monkeys (Shepherd et al., 2006). Such an equal rank

692   preference can be interpreted by the in-group effect. Similar ones can provide lessons and reference

693   for one's own behavior which increases the value of equal rank ones. In this way, although this social

694   class preference is not fixed, the reward signal underlying social status is always a key motivation in

695   social hierarchy interaction. These close correlations between social hierarchy and reward processing

696   allow us to understand the process of social hierarchy-related interaction from a more general

697   perspective. That is the link between social hierarchy stimuli — reward implied in the social

698   hierarchy information — valuation response.

699   **3. Information transfer and sharing: from SH-RL to SH-RI**

700   Although we view SH-RL and SH-RI as two independent processes in analyses to obtain clearer

701   results, these two psychological processes are clearly complementary (Qu et al., 2017). In daily life,

702   these two processes may be evoked in a cyclical manner. Knowledge of the social hierarchy would

703   allow an appropriate adjustment of behaviors for the subsequent interaction phase. This adjustment

704   can then be enhanced by the feedbacks of the environment or others post-interaction which can be

705   used to update information regarding the other individual (Santamaria-Garcia et al., 2014; Wittmann

706   et al., 2016). Or even learn others' social hierarchy via interaction somehow, and interaction process

707   includes an updating of social hierarchy. In this way, these two processes are not parallel but rather

708   connected and interactive. This connection implied a requirement of a bridge for communication

709   between these two processes that can transfer information about social hierarchy from the SH-RL to

710   SH-RI.

711   We found two regions, the amygdala, and hippocampus may contribute to this role. First, if some

712   brain regions are involved in both processes, the possibility that they contribute to the join points

713   would be higher than other brain areas. This assumption is fully backed by the results of conjunction

714   analysis, suggesting amygdala and hippocampus are overlappings between SH-RL and SH-RI.

715   Second, in the successive cognitive process of SH-RL, the action scope of the join points is more

716   likely to be located at the end of this overall cognitive stream. In other words, in terms of cognitive

717   functions involved in SH-RL, it is more reasonable that brain regions engaged in the construction and

718   representation of information are more likely involved in the transfer of this information to SH-RI,

719   rather than engaged in the initial detection or computation stages. The third reason relates to what we

720   previously discussed about the notion that the influence asymmetry of social hierarchy is generated by

721   differences in social value as a function of social rank. Therefore, brain regions involved in

722   connecting both processes should also be implicated in processing reward. This function can be used

723   to carry information about social hierarchy to regulate rewarding processing. In this view, it is

724   persuasive that the amygdala and hippocampus serve as join points between SH-RL and SH-RI.

725   Besides this finding in data analyses, this viewpoint can be supported by experimental evidence from

726   previous studies. In an fMRI study, participants learned some persons' and galaxies' ranks by

727   observational learning, then they were required to use their knowledge about the person and galaxy

728   hierarchies to decide how much in real monetary terms to pay for potential projects on offer in the

729   later interaction phase (Kumaran et al., 2012). Their fMRI results indicated that the activation of the

730   hippocampus as a function of person rank and galaxy rank (Kumaran et al., 2012). As to the amygdala,

731   they found a significant linear correlation between its neural activity and person rank, but not galaxy

732   rank (Kumaran et al., 2012). Another study that investigated both the learning phase and the

733   interaction phase observed domain-general coding of rank in the amygdala and hippocampus, even

734   when the interaction task was just required to categorize other persons according to the company to

735   which they belonged and not require the knowledge about their social hierarchy (Kumaran et al.,

736   2016). These experimental findings confirmed the role of the amygdala and hippocampus in

737   information transfer and sharing between SH-RL and SH-RI processes.

738   **4. Limitations**

739   The limitation related to the method should be discussed first. ALE meta-analysis utilizes partial

740   information of fMRI study, including the peak coordinates of brain activation and the number of

741   participants. Some other factors such as cluster size, effect size, scanning parameters are not taken

742   into account which also have their impacts on results and potential publication bias based on these

743   factors can not be obtained. Then, our study includes a couple of main limitations that should be

744   addressed in future studies. First, we treated SH-RL and SH-RI as two mutually independent yet

745   closely related cognitive processes in our current analyses. However, in some situations such as when

746   the social rank of another individual can not be assessed accurately at a time, these two processes may

747   invoke circularly and frequently. In this closed cognitive loop, the information transfer from SH-RL to

748   SH-RI is important. Based on our meta-analyses results, we proposed that the amygdala and

749   hippocampus may play a crucial role in transferring information from SH-RL to SH-RI. However, this

750   deduction is derived from data-driven analyses but lacks direct experimental evidence and needs

751   further investigations in the future.

752   Second, social hierarchy-related information exists in a dynamic social context, i.e., everyone

753   can be a sender or a receiver of the social hierarchical signal. Thus, investigating interpersonal

754   interactions by adopting a hyper-scanning approach that records signals from two or more participants

755   simultaneously is a meaningful research direction (Pinti et al., 2020). Since this proposed paradigm

756   needs further exploration, our identified brain regions could be used as regions of interest for future

757   studies employing, for example, functional near-infrared spectroscopy (fNIRS) based hyper-scanning

758   studies. Despite these limitations, we were able to gain valuable insight into the neural mechanism of

759   two key stages related to social hierarchy by combining a quantitative meta-analytical method with a

760   qualitative perspective.

761   **5. Conclusion**

762   In daily life, SH-RL and SH-RI are both essential to the efficient navigation of our social world. In

763   this study, we applied multiple meta-analytical methods to reveal the relevant neural mechanisms of

764   these processes. For SH-RL, we identified that AI and TPJ are likely implicated in detecting

765   dominance cues that carry information about social hierarchy; mPFC probably contributes to internal

766   updating and computing dynamic feedbacks; and that amygdala, hippocampus; and IPS possibly

767   serve to construct and represent a model of social hierarchy structure. For SH-RI, we found that this

768   process recruited the amygdala, hippocampus, striatum, and fusiform gyrus. Evidence of activation

769   pattern and function decoding revealed close links between SH-RI and reward processing, suggesting

770   the possibility that guidance by the reward processing network is the root mechanism underlying the

771   modulation of behavior in relation to social hierarchy. These results provide insights into the neural

772   signatures of social hierarchy-related learning and interaction. Considering social hierarchy as a basic

773   rule of society, these findings shed light on the understanding in interaction between social

774   organization and social cognition as well as some application for social adaptation in a

775   neuropsychological way.

776

777   **Supplementary Information**

778   Table S1.

779   Figure S1.

780   Figure S2.

781

782 **CRediT authorship contribution statement**

783 **Siying Li:** Conceptualization, Methodology, Formal analysis, Data Curation, Writing - Original Draft,

784 Writing - Review & Editing, Visualization. **Frank Krueger:** Methodology, Writing - Review &

785 Editing. **Julia A. Camilleri:** Methodology, Software, Formal analysis, Resources. **Simon B. Eickhoff:**

786 Methodology, Software, Resources. **Chen Qu:** Conceptualization, Writing - Review & Editing,

787 Supervision, Funding acquisition.

788

789 **Declaration of Competing Interest**

790 The authors declare no competing interests.

791

792 **Ethics statement**

793 The current work was a meta-analysis of existing data and there were no ethical considerations.

794

799

800 **References**

801   Amft, M., Bzdok, D., Laird, A. R., Fox, P. T., Schilbach, L., & Eickhoff, S. B. (2014). Definition and

802   characterization of an extended social-affective default network. *Brain Structure and*

803   *Function, 220*(2), 1031-1049. https://doi.org/10.1007/s00429-013-0698-0

804   Annis, J., & Palmeri, T. J. (2017). Bayesian statistical approaches to evaluating cognitive models.

805   *Wiley   Interdisciplinary   Reviews: Cognitive   Science,   9*(2),   e1458.

806   https://doi.org/10.1002/wcs.1458

807   Ashburner, J., & Friston, K. J., (2005). Unified segmentation. *Neuroimage, 26*(3), 839-851

808   https://doi.org/ 10.1016/j.neuroimage.2005.02.018

809   Baker, C. L., Jara-Ettinger, J., Saxe, R., & Tenenbaum, J. B. (2017). Rational quantitative attribution

810   of beliefs, desires and percepts in human mentalizing. *Nature Human Behaviour, 1*(4), 0064.

811   https://doi.org/10.1038/s41562-017-0064

812   Baxter, M. G., & Murray, E. A. (2002). The amygdala and reward. *Nature Reviews Neuroscience, 3*(7),

813   563-573. https://doi.org/10.1038/nrn875

814   Bellucci, G., Camilleri, J. A., Eickhoff, S. B., & Krueger, F. (2020). Neural signatures of prosocial

815   behaviors.   *Neuroscience   &   Biobehavioral   Reviews,   118,   186-195.*

816   https://doi.org/10.1016/j.neubiorev.2020.07.006

817   Berger, J., Rosenholtz, S. J., & Zelditch, M. (1980). Status Organizing Processes. Annual Review of

818   Sociology, 6(1), 479–508. https://doi.org/10.1146/annurev.so.06.080180.002403

819   Boksem, M. A. S., Kostermans, E., Milivojevic, B., & De Cremer, D. (2012). Social status determines

820   how we monitor and evaluate our performance. Social Cognitive and Affective Neuroscience,

821   7(3), 304-313. https://doi.org/10.1093/scan/nsr010

822   Bond, A. B., Kamil, A. C., & Balda, R. P. (2003). Social complexity and transitive inference in

823   corvids. *Animal Behaviour, 65*(3), 479-487. https://doi.org/10.1006/anbe.2003.2101

824   Boorman, E. D., O'Doherty, J. P., Adolphs, R., & Rangel, A. (2013). The Behavioral and Neural

825   Mechanisms Underlying the Tracking of Expertise. *Neuron, 80*(6), 1558–1571.

826   https://doi.org/ 10.1016/j.neuron.2013.10.024

827   Boyce, W. T. (2004). Social stratification, health, and violence in the very young. *Annals of the New*

828   *York Academy of Sciences, 1036*(1), 47-68. https://doi.org/10.1196/annals.1330.003

829   Bressler, S. L., & Menon, V. (2010). Large-scale brain networks in cognition: emerging methods and

830   principles. *Trends in Cognitiveences, 14*(6), 277–290.

831   https://doi.org/10.1016/j.tics.2010.04.004

832   Breton A, Jerbi K, Henaff M-A, Cheylus A, Baudouin J-Y, et al. (2014). Face the hierarchy: ERP and

833   oscillatory brain responses in social rank processing. *PLoS One, 9*(3), e91451.

834   https://doi.org/10.1371/journal.pone.0091451

835   Breton, A., Ligneul, R., Jerbi, K., George, N., Baudouin, J. Y., & Van Der Henst, J. B. (2019). How

836   occupational status influences the processing of faces: an EEG study. *Neuropsychologia, 122*,

837   125-135. https://doi.org/10.1016/j.neuropsychologia.2018.09.010

838   Brey, E., & Shutts, K. (2015). Children Use Nonverbal Cues to Make Inferences About Social Power.

839   *Child Development, 86*(1), 276-286. https://doi.org/10.1111/cdev.12334

840   Camilleri, J. A., Müller, V. I., Fox, P., Laird, A. R., Hoffstaedter, F., Kalenscher, T., & Eickhoff, S. B.

841   (2018). Definition and characterization of an extended multiple-demand network.

842   *NeuroImage, 165*, 138-147. https://doi.org/10.1016/j.neuroimage.2017.10.020

843   Charafeddine, R., Mercier, H., Clement, F., Kaufmann, L., Berchtold, A., Reboul, A., & Van der Henst,

844   J. B. (2015). How Preschoolers Use Cues of Dominance to Make Sense of Their Social

845   Environment. *Journal   of   Cognition   and   Development,   16*,   587-607.

846   https://doi.org/10.1080/15248372.2014.926269

847   Cheng, J. T., Tracy, J. L., Foulsham, T., Kingstone, A., & Henrich, J. (2013). Two Ways to the Top:

848   Evidence That Dominance and Prestige Are Distinct Yet Viable Avenues to Social Rank and

849   Influence. *Journal   of   Personality   &   Social   Psychology,   104*(1),   103-125.

850   https://doi:10.1037/a0030398

851   Chiao, J. Y., Adams, R. B., Tse, P. U., Lowenthal, L., Richeson, J. A., & Ambady, N. (2008). Knowing

852   Who's Boss: fMRI and ERP Investigations of Social Dominance Perception. *Group Processes

853   & Intergroup Relations, 11*(2), 201-214. https://doi.org/10.1177/1368430207088038

854   Chiao, J. Y., Harada, T., Oby, E. R., Li, Z., Parrish, T., & Bridge, D. J. (2009). Neural representations

855   of social status hierarchy in human inferior parietal cortex. *Neuropsychologia, 47*(2), 354-

856   363. https://doi.org/10.1016/j.neuropsychologia.2008.09.023

857   Christopoulos, G. I., Liu, X. X., & Hong, Y. Y. (2017). Toward an understanding of dynamic moral

858   decision making: model-free and model-based learning. *Journal of Business Ethics, 144*(4),

859   699-715. https://doi.org/10.1007/s10551-016-3058-1

860   Clos, M., Rottschy, C., Laird, A. R., Fox, P. T., & Eickhoff, S. B. (2014). Comparison of structural

861   covariance with functional connectivity approaches exemplified by an investigation of the

862   left   anterior   insula.   *NeuroImage,*   *99,*   269-280.

863   https://doi.org/10.1016/j.neuroimage.2014.05.030

864   Cloutier, J., Ambady, N., Meagher, T., & Gabrieli, J. D. E. (2012). The neural substrates of person

865   perception: Spontaneous use of financial and moral status knowledge. *Neuropsychologia,*

866   *50*(9), 2371–2376. https://doi.org/10.1016/j.neuropsychologia.2012.06.010

867   Cloutier, J., & Gyurovski, I. (2013). Intraparietal sulcus activity during explicit self-referential social

868   status judgments about others. *International Journal of Psychological Research, 6*, 68-79.

869   https://doi.org/10.21500/20112084.721

870   Cloutier, J., & Gyurovski, I. (2014). Ventral medial prefrontal cortex and person evaluation: Forming

871   impressions of others varying in financial and moral status. *Neuroimage, 100*, 535-543.

872   https://doi.org/ 10.1016/j.neuroimage.2014.06.024

873   Cohen Kadosh, R., Cohen Kadosh, K., Kaas, A., Henik, A., & Goebel, R. (2007). Notation-Dependent

874   and -Independent Representations of Numbers in the Parietal Lobes. *Neuron, 53*(2), 307–314.

875   https://doi.org/10.1016/j.neuron.2006.12.025

876   Constantinescu, A. O., Oreilly, J. X., & Behrens, T. E. J. (2016). Organizing conceptual knowledge in

877   humans   with   a   gridlike   code.   *Science,*   *352*(6292),   1464.

878   https://doi.org/10.1126/science.aaf0941

879   Crottaz-Herbette, S., & Menon, V. (2006). Where and when the anterior cingulate cortex modulates

880   attentional response: Combined fMRI and ERP evidence. *Journal of Cognitive Neuroscience,*

881   *18*(5), 766-780. https://doi.org/10.1162/jocn.2006.18.5.766

882   Cummins, D. D. (2000). How the social environment shaped the evolution of mind. *Synthese, 122*(1),

883   3-28. https://doi.org/10.1023/A:1005263825428

884   Dalmaso, M., Pavan, G., Castelli, L., & Galfano, G. (2011). Social status gates social attention in

885   humans. *Biology Letters, 8*(3), 450-452. https://doi.org/10.1098/rsbl.2011.0881

886   Deaner, R. O., Khera, A. V., & Platt, M. L. (2005). Monkeys pay per view: adaptive valuation of

887   social   images   by   rhesus   macaques. *Current   Biology,   15*(6),   543-548.

888   https://doi.org/10.1016/j.cub.2005.01.044

889   Decety, J., & Lamm, C. (2007). The role of the right temporoparietal junction in social interaction:

890   how low-level computational processes contribute to meta-cognition. *Neuroscientist, 13*(6),

891   580-593. https://doi.org/10.1177/1073858407304654

892   Dugatkin, LA. (1997). Winner and loser effects and the structure of dominance hierarchies.

893   *Behavioral Ecology, 8*(6), 583-587. https://doi.org/10.1093/beheco/8.6.583

894   Eickhoff, S. B., Bzdok, D., Laird, A. R., Kurth, F., & Fox, P. T. (2012). Activation likelihood

895   estimation meta-analysis revisited. *Neuroimage, 59*(3), 2349-2361. https://doi.org/10.1016/

896   j.neuroimage.2011.09. 017

897   Eickhoff, S. B., Bzdok, D., Laird, A. R., Roski, C., Caspers, S., Zilles, K., & Fox, P. T. (2011). Co-

898   activation   patterns   distinguish   cortical   modules,   their   connectivity   and   functional

899   differentiation. *Neuroimage,   57*(3),   938-949.

900   https://doi.org/10.1016/j.neuroimage.2011.05.021

901   Eickhoff, S. B., Laird, A. R., Grefkes, C., Wang, L. E., Zilles, K., & Fox, P. T. (2009). Coordinate-

based activation likelihood estimation meta-analysis of neuroimaging data: a random-effects approach based on empirical estimates of spatial uncertainty. *Human Brain Mapping, 30*(9), 2907-2926. https://doi.org/10.1002/hbm.20718

Eickhoff, S. B., Paus, T., Caspers, S., Grosbras, M. H., Evans, A. C., Zilles, K., & Amunts, K. (2007). Assignment of functional activations to probabilistic cytoarchitectonic areas revisited. *Neuroimage, 36*(3), 511-521. https://doi.org/10.1016/j.neuroimage.2007.03.060

Erk, S., Spitzer, M., Wunderlich, A. P., Galley, L., & Walter, H. (2002). Cultural objects modulate reward circuitry. Neuroreport, 13(18), 2499-2503. https://doi.org/10.1097/01.wnr.0000048542.12213.60

Fareri, D. S., & Delgado, M. R. (2014). Social Rewards and Social Networks in the Human Brain. *The Neuroscientist, 20*(4), 387-402. https://doi.org/10.1177/1073858414521869

Farrow, T. F., Jones, S. C., Kaylor-Hughes, C. J., Wilkinson, I. D., Woodruff, P. W., Hunter, M. D., & Spence, S. A. (2011). Higher or lower? The functional anatomy of perceived allocentric social hierarchies. *Neuroimage, 57*(4), 1552-1560. https://doi.org/10.1016/j.neuroimage.2011.05.069

Feng, C. L., Li, Z. H., Feng, X., Wang, L. L., Tian, T. X., & Luo, Y. J., 2016. Social hierarchy modulates neural responses of empathy for pain. *Social Cognitive and Affective Neuroscience, 11*(3), 485-495. https://doi.org/10.1093/scan/nsv135

Feng, C. L., Tian, T. X., Feng, X., & Luo, Y. J. (2015). Attention modulations on the perception of social hierarchy at distinct temporal stages: An electrophysiological investigation. *Neuropsychologia, 70*, 21-29. https://doi.org/10.1016/j.neuropsychologia.2015.02.013

923   Fernald, R. D. (2014). Communication about social status. *Current Opinion in Neurobiology, 28*, 1-4.

924   https://doi.org/10.1016/j.conb.2014.04.004

925   Fiske, S. T. (2012). Warmth and competence: Stereotype content issues for clinicians and researchers.

926   Canadian   Psychology/Psychologie   Canadienne,   53(1),   14–20.

927   https://doi.org/10.1037/a0026054

928   Freeman, J. B., Rule, N. O., Adams, R. B., & Ambady, N. (2009). Culture shapes a mesolimbic

929   response to signals of dominance and subordination that associates with behavior.

930   *Neuroimage, 47*(1), 353-359. https://doi.org/10.1016/j.neuroimage.2009.04.038

931   Friedman, D. P., Aggleton, J. P., & Saunders, R. C. (2002). Comparison of hippocampal, amygdala,

932   and perirhinal projections to the nucleus accumbens: combined anterograde and retrograde

933   tracing study in the macaque brain. *Journal of Comparative Neurology, 450*(4), 345-365.

934   https://doi.org/10.1002/cne.10336

935   FeldmanHall, O., & Shenhav, A. (2019). Resolving uncertainty in a social world. *Nature Human*

936   *Behaviour, 3*, 426-435. https://doi.org/10.1038/s41562-019-0590-x

937   Fudge, J., & Haber, S. (2001). Bed nucleus of the stria terminalis and extended amygdala inputs to

938   dopamine   subpopulations   in   primates.   *Neuroscience,   104*(3),   807-827.

939   https://doi.org/10.1016/S0306-4522(01)00112-9

940   Gilbert, P. (2000). The relationship of shame, social anxiety and depression: The role of the evaluation

941   of   social   rank.   *Clinical   Psychology   &   Psychotherapy,   7*(3),   174-189.

942   https://doi.org/10.1002/1099-0879(200007)7:3<174::Aid-Cpp236>3.0.Co;2-U

943   Gianaros, P. J., Horenstein, J. A., Hariri, A. R., Sheu, L. K., Manuck, S. B., Matthews, K. A., & Cohen,

944   S. (2008). Potential neural embedding of parental social standing. *Social Cognitive &*

945   *Affective Neuroscience, 3*(2), 91-96. https://doi.org/10.1093/scan/nsn003

946   Griffanti, L., Salimi-Khorshidi, G., Beckmann, C. F., Auerbach, E. J., Douaud, G., Sexton, C. E., ...

947   Smith, S. M. (2014). ICA-based artefact removal and accelerated fMRI acquisition for

948   improved resting state network imaging. *Neuroimage, 95*, 232-247. https://doi.org/

949   10.1016/j.neuroimage.2014.03.034

950   Grosenick, L., Clement, T. S., & Fernald, R. D. (2007). Fish can infer social rank by observation

951   alone. *Nature, 445*(7126), 429-432. https://doi.org/10.1038/nature05511

952   Gu, R. L., Huang, W. H., Camilleri, J., Xu, P. F., Wei, P., Eickhoff, S. B., & Feng, C. L. (2019). Love

953   is analogous to money in human brain: Coordinate-based and functional connectivity meta-

954   analyses of social and monetary reward anticipation. *Neuroscience & Biobehavioral Reviews,*

955   *100*(2019), 108-128. https://doi.org/10.1016/j.neubiorev.2019.02.017

956   Haaker, J., Molapour, T., & Olsson, A. (2016). Conditioned social dominance threat: observation of

957   others' social dominance biases threat learning. *Social Cognitive & Affective Neuroscience,*

958   *11*(10), 1627-1637. https://doi.org/10.1093/scan/nsw074

959   Haber, S. N., & Knutson, B. (2009). The Reward Circuit: Linking Primate Anatomy and Human

960   Imaging. *Neuropsychopharmacology, 35*(1), 4-26. https://doi.org/10.1038/npp.2009.129

961   Hampton, A. N., Bossaerts, P., & O"Doherty, J. P. (2008). Neural correlates of mentalizing-related

962   computations during strategic interactions in humans. *Proceedings of the National Academy*

963   *of Sciences of the United States of America, 105*(108), 6741-6746.

964   https://doi.org/10.1073/pnas.0711099105

965   Hardwick, R. M., Lesage, E., Eickhoff, C. R., Clos, M., Fox, P., & Eickhoff, S. B. (2015). Multimodal

966   connectivity of motor learning-related dorsal premotor cortex. *Neuroimage, 123*, 114-128.

967   https://doi.org/10.1016/j.neuroimage.2015.08.024

968   Horn, A., & Blankenburg, F. (2016). Toward a standardized structural–functional group connectome

969   in MNI space. *Neuroimage, 124*, 310-322. https://doi.org/10.1016/j.neuroimage.2015.08.048

970   Hu, J., Blue, P. R., Yu, H., Gong, X., Xiang, Y., Jiang, C., & Zhou, X. (2016). Social status modulates

971   the neural response to unfairness. *Social Cognitive & Affective Neuroscience, 11*(1), 1-10.

972   https://doi.org/10.1093/scan/nsv086

973   Hu, J., Cao, Y., Blue, P. R., & Zhou, X. (2014). Low social status decreases the neural salience of

974   unfairness. *Frontiers in Behavioral Neuroscience, 8*, 402.

975   https://doi.org/10.3389/fnbeh.2014.00402

976   Insel, T. R., & Fernald, R. D. (2004). HOW THE BRAIN PROCESSES SOCIAL INFORMATION:

977   Searching for the Social Brain. *Annual Review of Neuroscience, 27*(1), 697–722.

978   https://doi.org/10.1146/annurev.neuro.27.070203.144148 /fnbeh.2014.00402

979   Kedia, G., Mussweiler, T., & Linden, D. E. J. (2014). Brain mechanisms of social comparison and

980   their influence on the reward system. *Neuroreport, 25*(16), 1255-65. https://doi.org/

981   10.1097/WNR.0000000000000255

982   Khalvati, K., Park, S. A., Dreher, J.C., & Rao, R. P. N. (2016). A probabilistic model of social

983   decision making based on reward maximization. In Advances in Neural Information

984   Processing Systems (NIPS), pp. 2901–2909, Neural Information Processing Systems

985   Foundation.

986   Kim, P., Capistrano, C., & Congleton, C. (2016). Socioeconomic disadvantages and neural sensitivity

987   to infant cry: role of maternal distress. *Social Cognitive & Affective Neuroscience, 11*(10),

988   1597-1607. https://doi.org/10.1093/scan/nsw063

989   Kim, P., Evans, G. W., Angstadt, M., Ho, S. S., Sripada, C. S., Swain, J. E., . . . Phan, K.L. (2013).

990   Effects of childhood poverty and chronic stress on emotion regulatory brain function in

991   adulthood. *Proceedings of the National Academy of Sciences of the United States of America,*

992   *110*(42), 18442-18447. https://doi.org/10.1073/pnas.1308240110

993   Kim, P., Ho, S. S., Evans, G. W., Liberzon, I., & Swain, J. E. (2015). Childhood social inequalities

994   influences neural processes in young adult caregiving. Developmental Psychobiology, 57(8),

995   948–960. https://doi.org/10.1002/dev.21325

996   Kishida, K. T., Yang, D., Quartz, K. H., Quartz, S. R., & Montague, P. R. (2012). Implicit signals in

997   small group settings and their impact on the expression of cognitive capacity and associated

998   brain responses. *Philosophical Transactions of the Royal Society B: Biological Sciences,*

999   *367*(1589), 704-716. https://doi.org/ 10.1098/rstb.2011.0267

1000   Knill, D. C., & Pouget, A. (2004). The Bayesian brain: the role of uncertainty in neural coding and

1001   computation. *Trends   in   Neurosciences,   27*(12),   712-719.

1002   https://doi.org/10.1016/j.tins.2004.10.007

1003   Krall, S. C., Rottschy, C., Oberwelland, E., Bzdok, D., Fox, P. T., Eickhoff, S. B., . . . Konrad, K.

1004   (2015). The role of the right temporoparietal junction in attention and social interaction as

revealed by ALE meta-analysis. *Brain Structure & Function, 220*(2), 587-604. https://doi.org/10.1007/s00429-014-0803-z

Kraus, M. W., Torrez, B., Park, J. W., & Ghayebi, F. (2019). Evidence for the reproduction of social class in brief speech. *Proceedings of the National Academy of Sciences of the United States of America. 116*(46), 22998-23003. https://doi.org/ 10.1073/pnas.1900500116

Kumaran, D., Banino, A., Blundell, C., Hassabis, D., & Dayan, P. (2016). Computations Underlying Social Hierarchy Learning: Distinct Neural Mechanisms for Updating and Representing Self-Relevant Information. *Neuron, 92*(5), 1135-1147. https://doi.org/10.1016/j.neuron.2016.10.052

Kumaran, D., Melo, H. L., & Duzel, E. (2012). The Emergence and Representation of Knowledge about Social and Nonsocial Hierarchies. *Neuron 76*(3), 653-666. https://doi.org/10.1016/j.neuron.2012.09.035

Laird, A. R., Fox, P. M., Price, C. J., Glahn, D. C., Uecker, A. M., Lancaster, J. L., . . . Fox, P. T. (2005). ALE meta-analysis: Controlling the false discovery rate and performing statistical contrasts. *Human Brain Mapping, 25*(1), 155-164. https://doi.org/10.1002/hbm.20136

Lancaster, J. L., Tordesillas-Gutierrez, D., Martinez, M., Salinas, F., Evans, A., ZilleS, K., . . . Fox, P. T. (2007). Bias between MNI and talairach coordinates analyzed using the ICBM-152 brain template. *Human Brain Mapping, 28*(11), 1194-1205. https://doi.org/10.1002/hbm.20345

Langner, R., Rottschy, C., Laird, A. R., Fox, P. T., & Eickhoff, S. B. (2014). Meta-analytic connectivity modelling revisited: controlling for activation base rates. *NeuroImage, 99,* 559-570. https://doi.org/ 10.1016/j.neuroimage.2014.06.007

1026   Legates, T. A., Kvarta, M. D., Tooley, J. R., Francis, T. C., Lobo, M. K., Creed, M. C., & Thompson,

1027   S.M. (2018). Reward behaviour is regulated by the strength of hippocampus-nucleus

1028   accumbens synapses. *Nature, 564*(7735), 258-262. https://doi.org/10.1038/s41586-018-0740-

1029   8

1030   Ly, M., Haynes, R.M., Barter, J., Weinberger, D., & Zink, C. (2011). Subjective socioeconomic status

1031   predicts human ventral striatal responses to social status information. *Current Biology, 21*(9),

1032   794-797. https://doi.org/10.1016/j.cub.2011.03.050

1033   Ligneul, R., Obeso, I., Ruff, C. C., & Dreher, J. C. (2016). Dynamical Representation of Dominance

1034   Relationships in the Human Rostromedial Prefrontal Cortex. *Current Biology, 26*(23), 3107-

1035   3115. https://doi.org/10.1016/j.cub.2016.09.015

1036   Ligneul, R., Girard, R., & Dreher, J. C. (2017). Social brains and divides: the interplay between social

1037   dominance orientation and the neural sensitivity to hierarchical ranks. *Scientific Reports, 7,*

1038   45920. https://doi.org/10.1038/srep45920

1039   Lockwood, P. L., Wittmann, M. K., Apps, M. A., Klein-Flügge, M. C., Crockett, M. J., Humphreys, G.

1040   W., & Rushworth, M. F. (2018). Neural mechanisms for learning self and other ownership.

1041   *Nature Communications, 9*(1), 1-11. https://doi.org/10.1038/s41467-018-07231-9

1042   Marsh, A. A., Blair, K. S., Jones, M. M., Soliman, N., & Blair, R. J., 2009. Dominance and

1043   submission: the ventrolateral prefrontal cortex and responses to status cues. *Journal of*

1044   *Cognitive Neuroscience, 21*(4), 713-724. https://doi.org/10.1162/jocn.2009.21052

1045   Mattan, B. D., Kubota, J. T., & Cloutier, J. (2017). How social status shapes person perception and

1046   evaluation: a social neuroscience perspective. *Perspectives on Psychological Science, 12*(3),

468-507. https://doi.org/10.1177/1745691616677828

Mattan, B. D., Kubota, J. T., Dang, T. P., & Cloutier, J. (2018). External motivation to avoid prejudice alters neural responses to targets varying in race and status. *Social Cognitive & Affective Neuroscience, 13*(1), 22-31. https://doi.org/10.1093/scan/nsx128

Mason, M., Magee, J. C., & Fiske, S. T. (2014). Neural substrates of social status inference: Roles of medial prefrontal cortex and superior temporal sulcus. *Journal of Cognitive Neuroence, 26*(5), 1131-1140. https://doi.org/10.1162/jocn_a_00553

Mcgonigle, B. O., Chalmers, M., 1977. Are monkeys logical? *Nature, 267*(5613), 694-696. https://doi.org/ 10.1038/267694a0

Mcfarland, N. R., & Haber, S. N. (2002). Thalamic relay nuclei of the basal ganglia form both reciprocal and nonreciprocal cortical connections, linking multiple frontal cortical areas. *Journal of Neuroscience, 22*(18), 8117-8132. https://doi.org/10.1523/jneurosci.22-18-08117.2002

Menon, V. (2015). Salience Network. *Brain Mapping, 2*, 597–611. https://doi.org/10.1016/b978-0-12-397025-1.00052-x

Montagrin, A., Saiote, C., & Schiller, D. (2017). The social hippocampus. *Hippocampus, 28*, 672-679. https://doi.org/10.1002/hipo.22797

Muscatell, K. A., Dedovic, K., Slavich, G. M., Jarcho, M. R., Breen, E. C., Bower, J. E., … Eisenberger, N. I. (2016). Neural mechanisms linking social status and inflammatory responses to social stress. *Social Cognitive & Affective Neuroscience, 11*(6), 915-922.

1067   https://doi.org/ 10.1093/scan/nsw025

1068   Muscatell, K. A., McCormick, E., & Telzer, E. H. (2018). Subjective social status and neural

1069   processing of race in Mexican American adolescents. *Development and Psychopathology, 30*,

1070   1-12. https://doi.org/10.1017/S0954579418000949

1071   Nichols, T., Brett, M., Andersson, J., Wager, T., & Poline, J. B. (2005). Valid conjunction inference

1072   with the minimum statistic. *Neuroimage, 25*(3), 653-660. https://doi.org/

1073   10.1016/j.neuroimage.2004.12.005

1074   Noble, K. G., Wolmetz, M. E., Ochs, L. G., Farah, M. J., & McCandliss, B. D. (2006). Brain?

1075   behavior relationships in reading acquisition are modulated by socioeconomic factors.

1076   *Developmental Science, 9*(6). https://doi.org/10.1111/j.1467-7687.2006.00542.x

1077   Nooner, K. B., Colcombe, S., Tobe, R., Mennes, M., Benedict, M., Moreno, A., ... Milham, M. (2012).

1078   The NKI-Rockland sample: a model for accelerating the pace of discovery science in

1079   psychiatry. Front. *Frontiers in neuroscience, 6*(152), 1-11.

1080   https://doi.org/10.3389/fnins.2012.00152

1081   Op de Macks, Z. A., Bunge, S. A., Bell, O. N., Kriegsfeld, L. J., Kayser, A. S., & Dahl, R. E. (2017).

1082   The effect of social rank feedback on risk taking and associated reward processes in

1083   adolescent girls. *Social Cognitive & Affective Neuroscience, 12*(2), 240-250.

1084   https://doi.org/10.1093/scan/nsw125

1085   Olsson, A., Knapska, E., & Lindstrm, B. (2020). The neural and computational systems of social

1086   learning. *Nature Reviews Neuroscience, 21*(4), 197-212. https://doi.org/10.1038/s41583-020-

1087   0276-4

1088 Parkinson, C., Liu, S., & Wheatley, T. (2014). A common cortical metric for spatial, temporal, and

1089   social distance. *Journal of Neuroscience, 34*(5), 1979-1987.

1090   https://doi.org/10.1523/JNEUROSCI.2159-13.2014

1091 Paz-y-Miño C, G., Bond, A. B., Kamil, A. C., & Balda, R. P. (2004). Pinyon jays use transitive

1092   inference to predict social dominance. *Nature, 430*(7001), 778-781.

1093   https://doi.org/10.1038/nature02723

1094 Pinti, P., Tachtsidis, I., Hamilton, A., Hirsch, J., Aichelburg, C., Gilbert, S., & Burgess, P. W. (2020).

1095   The present and future use of functional near-infrared spectroscopy (fNIRS) for cognitive

1096   neuroscience. *Annals of the New York Academy of Sciences, 1464*(2018), 1-25.

1097   https://doi.org/10.1111/nyas.13948

1098 Qu, C., Ligneul, R., Van der Henst, J. B., & Dreher, J. C. (2017). An Integrative Interdisciplinary

1099   Perspective on Social Dominance Hierarchies. *Trends in Cognitive Sciences, 21*(11), 893-908.

1100   https://doi.org/10.1016/j.tics.2017.08.004

1101 Quirin, M., Meyer, F., Heise, N., Kuhl, J., Küstermann, E., Strüber, D., & Cacioppo. J.T. (2013).

1102   Neural correlates of social motivation: an fmri study on power versus affiliation.

1103   *International Journal of Psychophysiology, 88*(3), 289-295.

1104   https://doi.org/10.1016/j.ijpsycho.2012.07.003

1105 Roberts, W. A., & Phelps, M. T. (1994). Transitive inference in rats: a test of the spatial coding

1106   hypothesis. *Psychological Science, 5*(6), 368-374. https://doi.org/10.1111/j.1467-

1107   9280.1994.tb00287.x

1108 Robinson, J. L., Laird, A. R., Glahn, D. C., Lovallo, W. R., & Fox, P. T. (2010). Metaanalytic

connectivity modeling: delineating the functional connectivity of the human amygdala. *Human brain mapping, 31*(2), 173-184. https://doi.org/10.1002/hbm.20854

Rosvold, H. E., Mirsky, A. F., Pribram, K. H., 1954. Influence of amygdalectomy on social behavior in monkeys. *Journal of Comparative & Physiological Psychology, 47*(3), 173-178. https://doi.org/10.1037/h0058870.

Russchen, F. T., Bakst, I., Amaral, D. G., & Price, J. L. (1985). The amygdalostriatal projections in the monkey. an anterograde tracing study. *Brain Research, 329*(1-2), 241-257. https://doi.org/10.1016/0006-8993(85)90530-X

Salimi-Khorshidi, G., Douaud, G., Beckmann, C. F., Glasser, M. F., Griffanti, L., & Smith, S. M. (2014). Automatic denoising of functional MRI data: combining independent component analysis and hierarchical fusion of classifiers. *Neuroimage, 90*, 449-468. https://doi.org/10.1016/j.neuroimage.2013.11.046

Santamaria-Garcia, H., Pannunzi, M., Ayneto, A., Deco, G., & Sebastian-Galles, N. (2014). 'If you are good, I get better' : the role of social hierarchy in perceptual decision-making. *Social Cognitive & Affective Neuroscience, 9*(10), 1489-1497. https://doi.org/10.1093/scan/nst133

Santamaría-García, H., Burgaleta, M., & Sebastián-Gallés, N (2015). Neuroanatomical Markers of Social Hierarchy Recognition in Humans. a Combined ERP/MRI Study. *The Journal of Neuroscience, 35*(30), 10843-10850. https://doi.org/10.1523/JNEUROSCI.1457-14.2015

Satterthwaite, T. D., Elliott, M. A., Gerraty, R. T., Ruparel, K., Loughead, J., Calkins, M. E., …Wolf, D. H. (2013). An improved framework for confound regression and filtering for control of motion artifact in the preprocessing of resting-state functional connectivity data. *Neuroimage,*

1130   *64*(2013), 240-256. https://doi.org/10.1016/j.neuroimage.2012.08.052

1131 Sapolsky, R. M. (2005). The influence of social hierarchy on primate health. *Science, 308*(5722), 648-

1132   652. https://doi.org/10.1126/science.1106477

1133 Schafer, M., & Schiller, D. (2018). Navigating social space. *Neuron, 100*(2), 476-489.

1134   https://doi.org/10.1016/j.neuron.2018.10.006

1135 Seeley, W. W., Menon, V., Schatzberg, A. F., Keller, J., Glover, G. H., Kenna, H., ... Greicius, M. D.

1136   (2007). Dissociable intrinsic connectivity networks for salience processing and executive

1137   control. *The Journal of Neuroscience, 27*(9), 2349–2356.

1138   https://doi.org/10.1523/JNEUROSCI.5587-06.2007

1139 Seo, H., & Lee, D. (2017). Reinforcement learning and strategic reasoning during social decision-

1140   making. In Decision Neuroscience: An Integrative Perspective (Dreher, J.C. and Tremblay,

1141   L.,eds), pp. 225–231, Academic Press.

1142 Shepherd, S. V., Deaner, R. O., & Platt, M. L. (2006). Social status gates social attention in monkeys.

1143   *Current Biology, 16*(4), R119-R120. https://doi.org/10.1016/j.cub.2006.02.013

1144 Sheridan, M. A., Sarsour, K., Jutte, D., D'Esposito, M., & Boyce, W. T. (2012). The Impact of Social

1145   Disparity on Prefrontal Function in Childhood. *PLoS One, 7*(4), e35744. https://doi.org/

1146   10.1371/journal.pone.0035744

1147 Smith, R., Alkozei, A., & Killgore, W. D. S. (2016). Contributions of self-report and performance-

1148   based individual differences measures of social cognitive ability to large-scale neural

1149   network functioning. *Brain Imaging and Behavior, 11*(3), 685–697.

1150   https://doi.org/10.1007/s11682-016-9545-2

1151   Sterzer, P., & Kleinschmidt, A. (2010). Anterior insula activations in perceptual paradigms: Often

1152   observed but barely understood. *Brain Structure & Function, 214*, 611-622.

1153   https://doi.org/10.1007/s00429-010-0252-2

1154   Suzuki, S., Harasawa, N., Ueno, K., Gardner, J. L., & Nakahara, H. (2012). Learning to simulate

1155   others' decisions. *Neuron, 74*(6), 1125-1137.

1156   Swick, D., Ashley, V., & Turken, U. (2011). Are the neural correlates of stopping and not going

1157   identical? Quantitative meta-analysis of two response inhibition tasks. *Neuroimage, 56*(3),

1158   1655–1665. https://doi.org/10.1016/j.neuroimage.2011.02.070

1159   Tavares, R. M., Mendelsohn, A., Grossman, Y., Williams, C. H., Shapiro, M., Trope, Y., & Schiller, D.

1160   (2015). A Map for Social Navigation in the Human Brain. *Neuron, 87*(1), 231–243.

1161   https://doi.org/10.1016/j.neuron.2015.06.011

1162   Todorov, A., Said, C. P., Engell, A. D., & Oosterhof, N. N. (2008). Understanding evaluation of faces

1163   on social dimensions. *Trends in Cognitive Sciences, 12*(12), 455-460.

1164   https://doi.org/10.1016/j.tics.2008.10.001

1165   Turkeltaub, P. E., Eden, G. F., Jones, K. M., & Zeffiro, T. A. (2002). Meta-analysis of the functional

1166   neuroanatomy of single-word reading: Method and validation. *Neuroimage, 16*(3), 765-780.

1167   https://doi.org/10.1006/nimg.2002.1131

1168   Turkeltaub, P. E., Eickhoff, S. B., Laird, A. R., Fox, M., Wiener, M., & Fox, P. (2012). Minimizing

1169   within-experiment and within-group effects in activation likelihood estimation meta-analyses.

Human Brain Mapping, 33(1), 1-13. https://doi.org/10.1002/hbm.21186

Turner, J. A., & Laird, A. R. (2012). The cognitive paradigm ontology: design and application. *Neuroinformatics, 10*(1), 57-66. https://doi.org/10.1007/s12021-011-9126-x

Watanabe, N., & Yamamoto, M. (2015). Neural mechanisms of social dominance. *Frontiers in Neuroscience, 9*, 154. https://doi.org/10.3389/fnins.2015.00154

Wittmann, M. K., Kolling, N., Faber, N. S., Scholl, J., Nelissen, N., & Rushworth, M. F. S. (2016). Self-Other Mergence in the Frontal Cortex during Cooperation and Competition. *Neuron, 91*(2), 482–493. https://doi.org/10.1016/j.neuron.2016.06.022

Wong, T. Y., Sid, A., Wensing, T., Eickhoff, S. B., Habel, U., Gur, R. C., & Nickl-Jockschat, T. (2019). Neural networks of aggression: ALE meta-analyses on trait and elicited aggression. *Brain Structure & Function, 224*(1), 133-148. https://doi.org/10.1007/s00429-018-1765-3

Wu, P., Xia, B., Pienaar, J., & Zhao, X. (2014). The past, present and future of carbon labelling for construction materials – A review. Building and Environment, 77, 160–168. https://doi.org/10.1016/j.buildenv.2014.03.023

Xiang, T., Lohrenz, T., & Montague, P. R. (2013). Computational substrates of norms and their violations during social exchange. *Journal of Neuroscience, 33*(3), 1099-1108. https://doi.org/ 10.1523/JNEUROSCI.1642-12.2013

Zheng, Y., Cheng, X., Xu, J., Zheng, L., Li, L., Yang, G., & Guo, X. (2017). Proposers' economic status affects behavioral and neural responses to unfairness. *Frontiers in psychology, 8*, 847. https://doi.org/ 10.3389/fpsyg.2017.00847

1190   Zink, C. F., Tong, Y., Chen, Q., Bassett, D. S., Stein, J. L., & Meyer-Lindenberg, A. (2008). Know

1191   your place: neural processing of social hierarchy in humans. *Neuron, 58*(2), 273-283.

1192   https://doi.org/10.1016/j.neuron.2008.01.025

1193   Zitek, E. M., & Tiedens, L. Z. (2012). The fluency of social hierarchy: The ease with which

1194   hierarchical relationships are seen, remembered, learned, and liked. Journal of Personality

1195   and Social Psychology, 102(1), 98–115. https://doi.org/10.1037/a0025345